Assessing abundance trends of deep-diving cetaceans off Great Abaco Island in the Bahamas

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Surfacing male Blainville's beaked whale, *Mesoplodon densirostris* © Diane Claridge, BMMRO

DECLARATION OF ORIGINALITY

I, Sarah Dolman, herein declare that I have composed this thesis myself, that I have done the work here within and that all sources of information have been specifically acknowledged.

I further declare that this thesis has not been submitted in any previous application for a degree.

Signed

Date 20th August 2007

ABSTRACT

Concurrent with mid-frequency naval sonar use, seventeen cetaceans including fourteen beaked whales were found stranded on Great Abaco and surrounding Islands in the northern Bahamas in March 2000. This mass stranding caused an unknown mortality level and had an unknown impact on the distribution and survival of cetaceans in these waters, necessitating a requirement to monitor trends in the abundance of deep diving species. As a result, sighting surveys in adjacent deep coastal waters were conducted between July 2000 and November 2006 by the Bahamas Marine Mammal Research Organisation (BMMRO). This was the first analysis to investigate annual trends in abundance of dwarf sperm whales (*Kogia sima*), Blainville's beaked whales (*Mesoplodon densirostris*) and sperm whales (*Physeter macrocephalus*), the most commonly sighted oceanic species off Great Abaco Island. Generalised linear models (GLM) were fit to the sighting data in a Bayesian statistical framework to relate the observed whale counts to a series of explanatory covariates and to estimate annual trends in abundance. Sea state influenced estimates of dwarf sperm whales and Blainville's beaked whales, whilst the number of scientific observers influenced estimates of sperm whales. Julian day influenced dwarf sperm whale and sperm whale estimates, suggesting a seasonal effect. Estimated annual dwarf sperm whale and Blainville's beaked whale abundance decreased after 2000, whilst estimated sperm whale numbers in the study area were consistently low. A similar trend in the abundance estimates of dwarf sperm whales and Blainville's beaked whales coincided with an opposing trend for sperm whales. Possible causes for the occurrence of declining trends of dwarf sperm whales and Blainville's beaked whales in the study area include reductions in prey availability and the delayed impact of anthropogenic noise pollution. Increased efforts are required to further elucidate such declines. Ongoing survey effort is important to monitor the long-term abundance trends of deep diving cetaceans. Bayesian analysis provides the quantitative tools to facilitate such studies.

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INTRODUCTION

Deep diving species are among the most difficult cetaceans to study. The deep diving and offshore nature of cryptic species such as dwarf and pygmy sperm whales (*Kogiidae*) and beaked whales (*Ziphiidae*) has led to the belief that they are rare. Strandings have provided much of the available information on both *Kogiidae* and *Ziphiidae*. However, there are oceanic islands where deep waters can be easily accessed from shore using small vessels. The waters around the Bahamas represent one such location, and these waters have been the site of research on these enigmatic species since 1992.

This was the first analysis to investigate annual trends in abundance of dwarf sperm whales (*Kogia sima*), Blainville's beaked whales (*Mesoplodon densirostris*) and sperm whales (*Physeter macrocephalus*) between July 2000 and November 2006. Visual sightings data were fit with a generalised linear model (GLM) to relate the observed whale counts to a series of explanatory covariates in order to explain as much variability in the estimates as possible and to estimate annual trends.

To set this analysis in context, background is provided on i). A noise related mass mortality event that led to collection of standardised data for assessing abundance trends; ii). Challenges associated with the study of deep diving cetaceans, iii). An introduction to dwarf sperm whales, Blainville's beaked whales and sperm whales; and, iv). Bayesian statistical analysis.

Mass mortality event that preceded standardised data collection

Documented mortalities of *Kogia, Ziphiidae* and sperm whales have included fisheries interactions, hunting, vessel collisions and ingestion of plastic and fish hooks (for example, Gomerčić *et al.,* 2005; Ohizumi *et al.,* 2003; Carrillo, 2003; Alpine, 2002; Poncelet *et al.,* 2000; Read and Wade, 2000; Cardona-Maldonado and Mignucci-Giannoni, 1999; Willis and Baird, 1998). However, interest in populations of deep diving whales has been focused with concerns regarding noise pollution (Hildebrand, 2005; Fernandez *et al*., 2005; 2004; Hooker *et al.,* 2002a; Frantzis, 1998; Simmonds and Lopez-Jurado, 1991; Van Bree and Kristensen, 1974). In particular, mass mortality events, coincident to anthropogenic noise pollution and usually including beaked whales, have taken place around the world. Fourteen beaked whales (including nine Cuvier's (*Ziphius cavirostris*) and one Blainville's beaked whale) were found stranded on islands surrounding the Bahamas study area in March 2000 (Balcomb and Claridge, 2001). The stranding event occurred concurrent to the operation of mid-frequency naval sonar during the transit of numerous multi-national naval vessels through the Northwest Providence Channel (Anon., 2001) to the south of the Islands of Great Abaco and Grand Bahama (Figure 1). This stranding caused an unknown mortality level and had an unknown influence on the survival and area usage of the cetaceans in these waters. Previous data were collected opportunistically using boat surveys targeting known cetacean hot spots. The potential population impacts of the stranding led to a systematic survey approach to enable repeatable assessment of distribution, abundance and trends of study species.

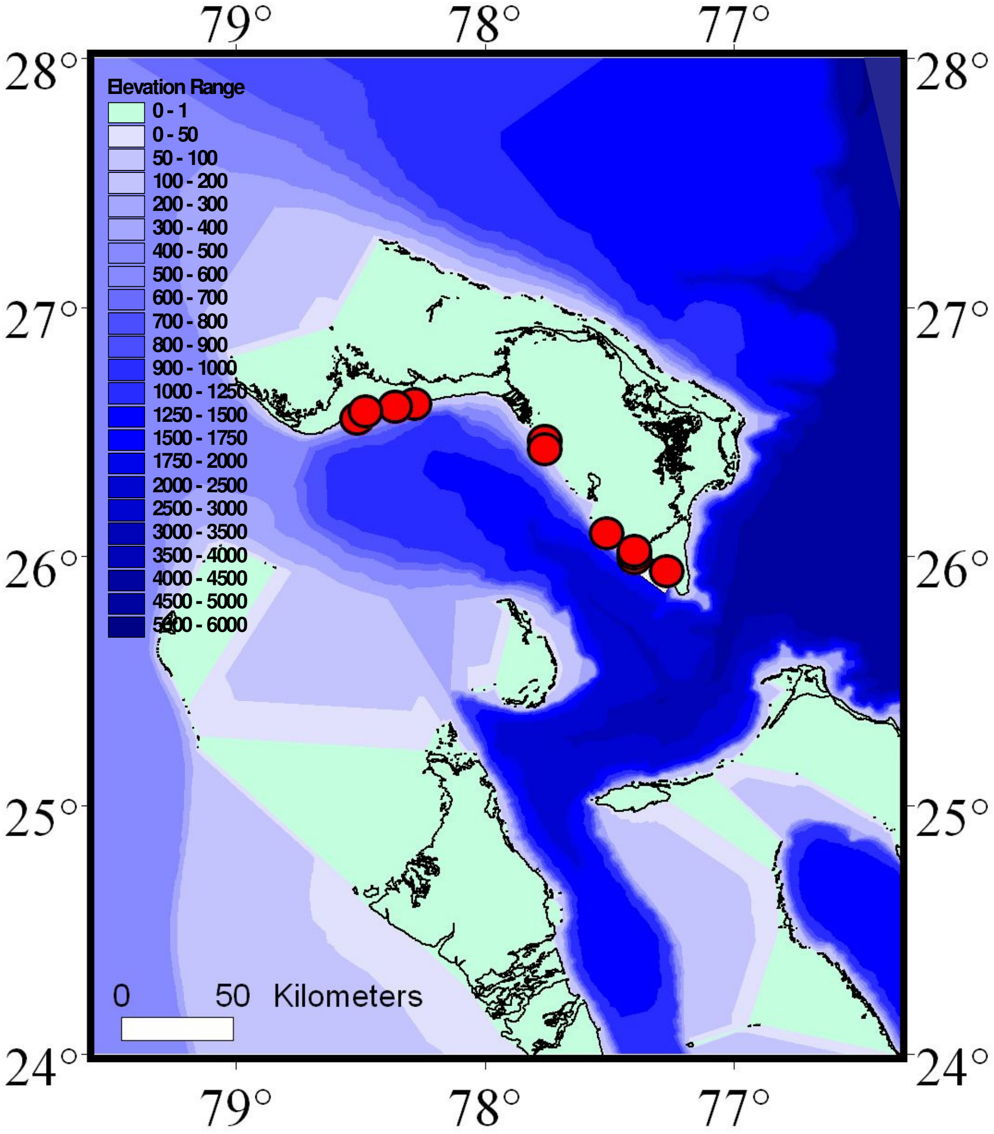

Figure 1. Map of the northern Bahamas, including stranding locations of fifteen beaked whales in March 2000. Depth information from GEBCO Digital Atlas (geographic projection). Depth coutours in metres.

Population and abundance assessment

Effective conservation efforts require knowledge of population range and size (Elith *et al.,* 2006; Durban and Elston, 2005) and trends over time (Cañadas *et al.,* 2005; Austin, 2002). Different field survey approaches exist that provide different measures of population size, relative or absolute abundance, or density (Hammond, 2001). Careful consideration of field survey design and the assumptions inherent in estimation methods are required, depending on the study species (Parra *et al.,* 2006).

Cuvier's beaked whales demonstrated a high degree of isolation and low maternal gene flow in an investigation of population genetic structure amongst oceanic and, in some cases, regional populations (Dalebout *et al.,* 2005). Another study showed the Gully to be a unique ecosystem which harbours a distinct population of Northern bottlenose whales (*Hyperoodon ampullatus*) in the western North Atlantic (Dalebout *et al.,* 2006). Limited gene flow has been documented for beaked whales studied within the Hawaiian Islands (McSweeney *et al.,* 2007). Whilst these studies are suggestive of distinctive populations of other beaked whale species at least, nothing is known about the regional or local populations of dwarf sperm whales and Blainville's beaked whales, thereby constraining attempts to identify relevant biological populations. With such population data lacking, area-specific abundance estimation currently provides a necessary focus.

Abundance estimates have been produced for deep diving cetacean species in the Southern Ocean (Kasamatsu and Joyce, 1995), off Japan (Miyashita and Kato, 1993; Miyashita, 1986), around the US (see Barlow *et al.,* 2006) and in the North Atlantic (Buckland *et al.,* 1993; Sigurjónsson *et al.,* 1991; 1989). However, Barlow and Gisiner (2006) stated that surveys to detect population-wide declines in beaked whale abundance do not hold much promise in the short term due to lack of precision in estimates of population sizes, resulting from a small sample size of observations. Significantly, Taylor *et al.* (2007) found in a review of US large-ship surveys that the percentage of precipitous declines that would *not* be detected for beaked whales was 90% (where a precipitous decline was determined as a 50% decrease in abundance in 15 yr). These approaches to abundance estimation are therefore clearly not suitable to accurately assess changes in abundance of deep diving small whales.

Given these constraints, alternative approaches to assessing abundance trends in deep diving oceanic cetaceans are required. One such approach is to use a relative measure or 'index' of population density over time. An index can inform us of changes in abundance, without knowing the actual size of the population, assuming proportionality is constant (Schwartz and Seber, 1999). Indeed, Taylor *et al.* (2007) supported designing surveys with the aim of detection of trends in abundance, rather than absolute abundance. Further, Bayesian methods were promoted for trend analysis, owing to their ability for inclusion of prior information, and the advantage of producing probability distributions that can be used in formal decision analysis (Taylor *et al.,* 2007). An index may be the most efficient means of addressing population monitoring objectives (Engeman, 2003). Indices are often used for species that are difficult to capture or observe directly (Williams *et al.,* 2002). For elusive and little known species, such as dwarf sperm whales and Blainville's beaked whales, it might only be possible to measure abundance trends within a designed study area of interest such as that off Great Abaco Island.

Despite their oceanic nature, dwarf sperm whales and Blainville's beaked whales are the most frequently sighted species in pelagic waters off Great Abaco Island (this study; Claridge, 2006; MacLeod *et al.*, 2004). Sperm whales are the third most sighted oceanic species (Claridge, 2006). Cuvier's beaked whales and Blainville's beaked whales are the most commonly encountered species off El Hierro in the Canary Islands (Aguilar Soto, 2006). Dwarf sperm whales are one of the most commonly sighted species in the oceanic northern Gulf of Mexico (Mullin and Fulling, 2004) and are frequently sighted during small boat surveys off Hawaii (Baird *et al.,* 2006) and around the Maldives (Anderson, 2005). These deep diving species may therefore not be so much rare as elusive because of their deep-diving habits and oceanic habitat. This, and other factors, poses a considerable challenge in their study.

Challenges with studying deep diving species

The deep-diving foraging nature of dwarf sperm whales, Blainville's beaked whales and sperm whales means that they spend considerable time foraging at depth with only limited periods resting at the surface. This behaviour provides a unique challenge to assessment of abundance indices let alone population abundance and distribution. Whilst sperm whales provide a recognisable visible cue with a large bushy blow and regular logging behaviour, both dwarf sperm whales and Blainville's beaked whales provide limited visual cues, and at short distances (McSweeney *et al.,* 2007; Claridge, 2006). Both *Kogiidae* and *Ziphiidae* are challenging to identify at sea to species level, further challenging abundance estimation.

For survey data to be useful for detecting abundance trends, counts must provide a reliable index of the number of animals in the area (Thompson *et al.,* 1997). In order to accurately determine abundance trends, survey methods should be standardised and factors that influence detection and sightability should be included in statistical analysis where possible. Key factors influencing detection of dwarf sperm whales, Blainville's beaked whales and sperm whales are discussed below.

Potential factors affecting detection

Pollock *et al.* (2002) described approaches to try and deal with failure of detectability (catchability, sightability, observability) in detail, including survey design, measurement of covariates that may influence detectability, model adjustment and acknowledgement of model limitations. Three classes of variables affect probability of detection and these are related to the observer, the environment and the species itself (Barlow *et al.,* 2001; Anderson, 2001). Meaningful relationships should be identified in an ecological model (Ferguson and Barlow, 2005) and where possible appropriate covariates incorporated. Appropriate covariates are those that define relationships with the aim of refining study methodology and ultimately providing guidance on future field survey efforts. The following covariates were included in analysis conducted in this study.

Observers

Sightings rates of experienced cetacean observers are twice those of inexperienced observers (Barlow *et al.,* 2006). The number of scientific observers on board a survey may be a factor that affects detection. During this study, the number and experience of observers varied for each transect completed, and were thus categorised into scientists, research assistants and volunteers. Volunteers were considered to become research assistants, and assistants to become scientists after completion of a full field season, unless considerable experience was obtained elsewhere. To account for such observer differences, a covariate was introduced to the analysis to incorporate observer training and experience. Because sightings were invariably made by the experienced scientists, and observations were only recorded where they were verified by a scientist, data on the total number of observers on board were discarded in favour of a count of the number of scientists on board the vessel during transects.

Environment

Sea state

Environmental conditions influence visual observations of cetaceans. Detection of small whales with low surface profiles is strongly determined by sea state (Barlow, 2006; Claridge, 2006; Baird, 2005; Clarke, 1982). In the study area, detection is generally limited to calm waters (sea state 0-2) for small beaked whales (Claridge, 2006) and *Kogia* (Dunphy-Daly *et al.,* in press). For this reason, during this study transect surveys were only conducted in sea state < 3 to maximise encounter opportunities and were completed if the sea increased to sea state 3 during the last of six legs. Sea state was included as a covariate to determine if variability between 0, 1 and 2 influenced whale counts.

Survey start time

Clark (1982) reported sun glare, which can seriously impair detections over part of the search arc as the sun rises and falls during the day, as a factor affecting the detection of cetaceans. Sun glare, in combination with cloud cover, can be expected to affect detection rates as the sun travels its path uniformly on a daily basis. Intensity can be expected to increase when the sun is high in the sky during the mid part of the day. Survey start time (using the 24 hr clock) was included as a covariate as a proxy for sun glare, which itself was determined difficult to incorporate with the data available.

Species

Julian day

Many cetacean species undertake seasonal movements and so we may expect seasonal variations in temporal occurrence patterns within the study area. Seasonal movements have been documented in dwarf sperm whale (Dunphy-Daly *et al.,* in press; Willis and Baird, 1998) and sperm whale (Whitehead, 2003) populations. This was incorporated through a covariate for the dates on which completed transects were undertaken, specified in terms of julian day (where January 1st to December 31st ranged from 001 to 365).

Dwarf sperm whale, *Kogia Sima* (Owen, 1866)

Figure 2. Dwarf sperm whale, *Kogia sima*. Illustration by Martin Camm

Dwarf sperm whales (Figure 2) are small (averaging 2.7 m: Bloodworth and Marshall, 2003) oceanic cetaceans inhabiting temperate and tropical waters world-wide. Willis and Baird (1998) provide a full list of documented records. Although described as two species (*Kogia sima* and *K. breviceps*: Yamada, 1954), a second species of *Kogia sima* may be determined in future (Chivers *et al.,* 2005). The global population of dwarf sperm whales is recognised as being Lower Risk (Least Concern) under the IUCN (World Conservation Union) Red List of Threatened Species (IUCN, 2006).

In some regions, dwarf sperm whale populations appear separated into age-classes. Juvenile and immature animals occur closer inshore than adults, inhabiting waters over the outer part of the continental shelf and upper part of the slope (Ross, 1984). Seasonal onshore-offshore movements and changes in group size have been demonstrated within the Great Abaco Island study area (Dunphy-Daly *et al*., in press).

Baumgartner *et al.* (2001) suggested that *Kogia* may associate with frontal regions along the shelf break and the upper continental slope, since these are areas with high epipelagic zooplankton biomass. Dwarf sperm whales feed inshore of pygmy sperm whales (Wang *et al*., 2002; Willis and Baird, 1998). Strandings data have enabled the analysis of stomach contents. Both *Kogia* species are primarily Teutophagous, with diet consisting mainly of 11 families of cephalopods, as well as fish and crustaceans (Clarke, 1996). Predation of dwarf sperm whales by killer whales (*Orcinus orca*) has been observed in the study area (Dunn *et al.,* in prep.).

Blainville's beaked whale, *Mesoplodon densirostris* (de Blainville, 1817)

Figure 3. Male Blainville's beaked whale, *Mesoplodon densirostris*. Illustration by Martin Camm

Figure 4. Female Blainville's beaked whale, *M. densirostris*. Illustration by Martin Camm

Like dwarf sperm whales, Blainville's beaked whales inhabit temperate and tropical oceanic waters. Blainville's beaked whales are medium-sized odontocetes (males reach 5.5 m in length (Figure 3) and females reach 4.7 m (Figure 4): Klinowska, 1991). No genetic studies have been completed for Blainville's beaked whales and wide-scale movements are currently unknown. However, photographic re-sightings suggest a high level of site fidelity of some individuals within the study area (Claridge, 2006) and Hawaii (McSweeney *et al.,* 2007).

Around some oceanic islands, Blainville's beaked whales are found in shallower, inshore waters than Cuvier's beaked whales (Bahamas: Claridge, 2006; MacLeod *et al.,* 2004; Hawaii: Baird *et al.,* 2004). Blainville's beaked whales demonstrate female defense polygamy (McSweeney *et al.,* 2007; Claridge, 2006) and sub-adults have been found in deeper, offshore waters, suggesting a dominancy hierarchy (Claridge, 2006). Differences in occupancy patterns have also been reported, with a higher turnover of males than females in coastal waters within the study area (Durban *et al.*, 2001).

Stomach contents were collected from a number of beaked whales that stranded on the Canary Islands immediately following a naval exercise. This event provided the unique opportunity to investigate the full stomachs of previously healthy individuals, including that of a Blainville's beaked whale. Stomach contents included otoliths and bones of fish belonging to the families *Gadidae* and *Myctophidae*. Beaks from five cephalopod taxa: *Octopoteuthis sicula*, *Histioteuthis reversa*, *H. meleagroteuthis*, *Histioteuthis* Type A and *Taonius pavo*, cephalopod eye lenses and the remains of one crustacean were found in the stomach (Santos *et al.,* 2007).

Sperm whale, *Physeter macrocephalus* (Linneaus, 1758)

Figure 5. Sperm whale, *Physeter macrocephalus*. Illustration by Martin Camm

Sperm whales (Figure 5) are large and sexually dimorphic, with males reaching 16 m and females reaching 11 m, and are found in all deep, ice-free waters (Rice, 1989). Whilst much uncertainty surrounds population levels, global population size has been estimated at 360,000 whales and is predicted to be about 32% of pre-whaling size (Whitehead, 2002). The global population of sperm whales is recognised as being Vulnerable under the IUCN Red List (IUCN, 2006).

Male sperm whales head for polar waters with the onset of puberty and form bachelor herds, returning to the tropics in adulthood (Rendell and Whitehead, 2005). Females and their young form groups of ~20 animals and range widely in tropical and subtropical waters (Whitehead, 2001), and are typically the age sex classes found in the Bahamas (Durban, pers. comm.). Sperm whale populations show little genetic structure (Whitehead, 2002) but exhibit cultural variation in foraging behaviour (Marcoux *et al.,* 2007) as well as local vocal dialects (Rendell and Whitehead, 2005). Differences in foraging behaviour have been observed between clans and are reflected in the prey consumed (Marcoux *et al.,* 2007). Age-related changes in feeding grounds have been demonstrated using stable isotope analysis and a higher fish intake has been demonstrated in higher latitudes (Ruiz-Cooley *et al.,* 2004). However, dominant prey species include *Ommastrephidae*, *Onychoteuthidae* and *Octopoteuthidae* (Clarke, 1996).

Bayesian Statistics

Mathematician Reverend Thomas Bayes first conceived Bayesian methods in 1763 and the method dominated statistical thinking through the nineteenth century (Brooks, 2003). However, complex calculus prevented their widespread practical use until recent years. Re-emergence of Bayes Theorem began in the 1980s with the development of sophisticated computational tools that have enabled analysis of complex problems using numerical approximation and simulation techniques (Fryback *et al.,* 2001).

Comparisons of classical (frequentist) and Bayesian statistical methods in ecology have resulted in identification of strengths and weaknesses for each method (for example, Wade, 1999). There is still much controversy surrounding the philosophical merits of the two approaches (for example, Dennis, 1996). However, mathematicians and ecologists now move between the philosophies as a matter of convenience, and the Bayesian approach has proved powerful in many practical settings (for example, Durban *et al.,* 2005; Thompson *et al.,* 2005; Brooks, 2003; Fleishman *et al.,* 2001; Durban *et al.*, 2000; Wade, 1999; Madigan and York, 1997; Ellison, 1996). The broader benefits and limitations of Bayesian statistics have been summarised (Table 1).

Table 1. Benefits and limitations of Bayesian statistics (from McCarthy, 2007; O'Hagan and Luce, 2003; Wade, 2000 and other sources where cited)

Benefits	Limitations
Explicit use of prior information (including uncertainty and expert knowledge) can be seen as both a benefit and a limitation (Asseburg, 2006)	
Pre-existing information can be used quantitatively (Ellison, 1996)	Introduces an element of subjectivity (although this is treated explicitly)
Can incorporate missing data (Uusitalo, 2007)	Difficulties in constructing or specifying priors
Enables direct evaluation of the probability of alternative scientific hypothesis (Durban, 2002)	Limited ability to deal with continuous data (Uusitalo, 2007)
Can provide accurate predictions with small sample sizes (Uusitalo, 2007)	Limited guidance for presentation of Bayesian analysis (Anderson *et al.,* 2001)
Can be used to infer biological significance as well as statistical significance (McCarthy and Parris, 2004)	Bayesian methods are not commonly taught in ecology
Ability to update the model to incorporate new data makes it useful for adaptive management (Asseburg, 2006; Ellison, 1996)	
Modern computation allows easy analysis of complex models	
Allows for intuitive interpretation of probabilities and hence ease of application to decision making	

Both frequentist and Bayesian methods are based on a likelihood function – a probability model for the observed data given parameter values. However, rather than finding a single set of parameter values that give the highest likelihood, as in frequentist methods, the Bayesian approach evaluates the likelihood across a full distribution of prior parameter values. The result is the 'posterior distribution' which conveys uncertainty about parameters in the logical language of probability or chance (Durban, 2002). Bayesian analyses therefore begin by setting a prior distribution on each parameter. These priors are intended to be subjective, typically based upon expert knowledge or past studies. The process of updating prior distributions to form posteriors is very natural for iterative studies, where a cyclical combination of old and new data through application of the model can then be used for future iterations. This process is increasingly used in environmental decision making and is known as adaptive management. Although concerns have been expressed about Bayesian priors, they do allow relevant prior information to be formally incorporated into analyses. Furthermore, subjective choice of prior has been identified as being similar to the problem of choosing a significance level for the frequentist hypothesis test (Brooks, 2003). An alternative and more contemporary approach is to use flat or non-informative prior distributions, and this is the approach adopted in this study.

Confidence limits and hypothesis testing used in frequentist approaches allow for little flexibility in dynamic, changing situations (Ellison, 1996). However, the utility of probability as a language for dealing with uncertainty means that Bayesian techniques are particularly relevant in ecological terms because of the direct applicability of conveying uncertainty to conservation and management decisions (Wade, 1999). Bayesian analysis is increasingly a favoured technique for conservation orientated science where precise population parameters can never be known, yet management decisions have to be made. Probabilistic predictions can also aid decision makers who do not have an ecological or scientific background. Notably, Bayesian techniques have been prominently used in fisheries stock assessments (e.g. Maunder *et al.,* 2000; Punt and Hilborn, 1997). Bayesian techniques have been used to calculate population estimates of bottlenose dolphins (*Tursiops truncatus*) (Durban *et al.,* 2005), to assess the effectiveness of spatio-temporal protection of endangered Hector's dolphins (*Cephalorhynchus hectori*) (King and Brooks, 2004), to assess trends in harbour seal (*Phoca vitulina richardsi*) populations following the Exxon Valdez oil spill in Alaska (Ver Hoef and Frost, 2003) and to facilitate management of Bowhead whale (*Balaena mysticetus*) populations under International Whaling Commission (IWC) management (Givens, 1999; Raftery *et al.,* 1995). A general framework for Bayesian modelling of dynamic processes of managed wildlife populations has recently been developed (Buckland *et al.,* 2004).

Model limitations

Modelling is undertaken to link observations to key model parameters which can be estimated. These estimates can then be used to make inference about population parameters such as abundance and trends, to explore the consequences of future management decisions, and to estimate the probability of extinction (Wade, 1999). Model-based inference is unlikely to perfectly reflect real processes, but it does allow observations to be used in formal and structured analyses to abstract the key features of the system. Furthermore, the performance of each model can be investigated to assess the validity of the inherent assumptions and therefore it's utility to ecological inference. However, it is important to remember that a model can never fully incorporate all key variables and so will never provide truly accurate results (Durban, 2002).

When modelling estimates of whales, factors suspected to affect detection should be incorporated into analysis where possible. Therefore, models were developed that incorporated covariates likely to have a causal effect on observations. This enabled investigation of relationships between estimates of whales and covariates, but more importantly to account for these sources of variability when assessing annual abundance indices. Nonetheless, influential covariates are themselves of interest and can demonstrate seasonal movements, for example, and also guide future data collection to optimise sighting conditions.

Care must be taken with determining management decisions based on the outputs of a model, and emphasis must be placed on quantifying and communicating uncertainty. For example, despite this being an unprecedented dataset for dwarf sperm whales and Blainville's beaked whales, the nature of the species and difficulties in their study means that the sample size of each species is small. In addition, there is considerable variation in effort between years. Consequently, there is likely to be considerable uncertainty associated with parameter estimates and statistical inference. However, a Bayesian statistical approach was adopted, where uncertainty about model parameters is analysed and communicated as discrete probability distributions (Wade, 1999).

Bayesian models were developed to estimate annual trends in abundance of deep diving dwarf sperm whales, Blainville's beaked whales and sperm whales off Great Abaco Island between July 2000 and November 2006. A Poisson generalised linear model (GLM) was developed to examine the relationship between the observed whale counts and a series of continuous explanatory covariates: julian day, sea state, survey start time and number of scientists, as well as a parameter to describe the idealised count for each year under optimal conditions (annual index). Each covariate was incorporated to explain as much of the variability in the counts as possible, to facilitate inference about the annual index.

METHODS

Study area

Great Abaco Island is situated upon a shallow carbonate bank in the north of the Bahamas archipelago in the tropical western Atlantic Ocean. The Great Bahama Canyon sweeps down the western side of the Island, splitting the northeast and Northwest Providence Channel, and coming within 3 km of shore in the study area. The canyon has steep upper slopes (Mullins *et al.,* 1984) and a depth of 4,285 m to the ocean floor.

The study area is situated off the southern end of Great Abaco Island (Figure 6). It encompasses 126nm² of habitat ranging from shallow gently sloping sandy bottom to steep walled canyons and depths of 2 m to 1,600 m (Dunphy-Daly *et al.,* in press).

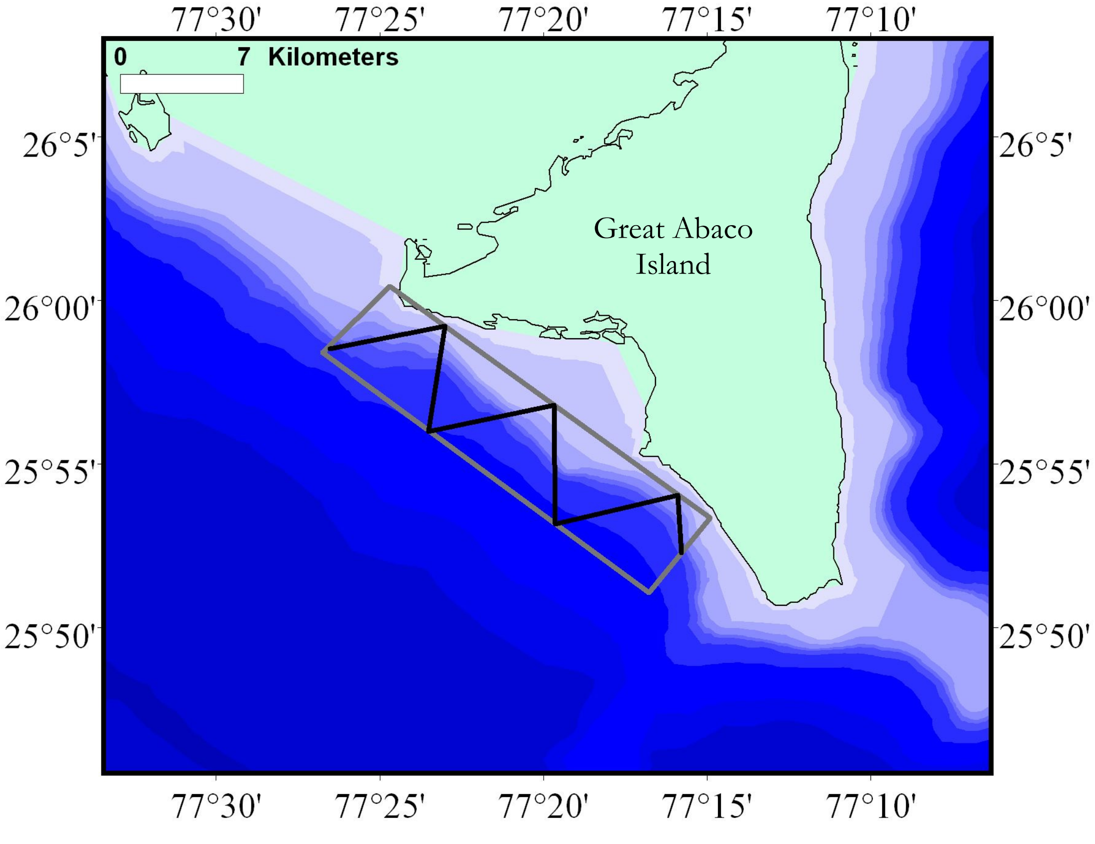

Figure 6. Map of the study site off southern Great Abaco Island, Bahamas.
Depth information from GEBCO Digital Atlas (geographic projection). Depth contours are a guide only.

The Bahamas climate is sub-tropical. Seasonal weather shifts from southward-moving polar air during the winter to warm moist northwards-moving air from the Caribbean during the summer (Buchan, 2000). The low-lying islands are subject to significant and variable hurricane and storm activity between August and October (Buchan, 2000). Currents that influence the temperature and subsequent productivity of the Bahamas waters come predominantly from the constant Gulf Stream from the west, the Deep Western Boundary Current (DWBC) which meanders beneath it (Meinen *et al.,* 2004) and the annually and seasonally variable Antilles Current. The Antilles Current moves westwards from Africa towards the more northerly Bahamas islands in summer and towards the more southerly islands during winter (Buchan, 2000). Levels of primary productivity around the Bahamas are generally low, at less than 6 mg m^{-2} (Longhurst, 1998, cited in MacLeod and Zuur, 2005).

Field methods

Randomised saw-toothed line-transect surveys were conducted within a fixed rectangular grid south of Great Abaco Island between July 2000 and November 2006. The grid is 6 km wide by 21 km long (Dunphy-daly *et al.,* in press) and runs parallel to the slope of the canyon wall. The transect lines were drawn to start along one of the two short ends of the rectangular survey grid, and to begin in either an upwards or downwards direction. On reaching the edge of the grid, a new transect leg would begin, at an angle of 70 degrees to the previous leg. Each completed transect therefore consisted of an average of six legs, running across the slope of the canyon wall, averaging 19.2 nautical miles in total. Even for small whales, sighting distances can be as great as 4.88 km (breaching Blainville's beaked whale), with a mean sighting distance of all species of 0.87 km (Claridge, 2006). Therefore each saw-tooth transect provided a good level of the coverage of the grid. Map of a completed transect is shown (Figure 6). Two small (< 7 m) rigid inflatable boats (RIBs) were used, *RV Chimo* and *RV Zip*, with a survey platform observation height of 2 – 2.5 m, travelling at a constant survey speed of approximately 15 kn. Claridge (2006) fully describes line transect design and survey protocols. No more than one transect was completed in a day and only completed transects were incorporated into the analysis. From two to ten observers, including between none and three scientists, scanned with naked eyes for 360° around the vessel and conducted occasional sweeps with 7 x 50 binoculars.

Both closing and passing modes were undertaken, often closing for observations of species other than *Kogia*, whose elusive behaviour makes prolonged encounters difficult. At the end of an encounter during closing mode, full effort was resumed once the vessel had returned to the recorded transect break position. All cetaceans identified were recorded to lowest taxonomic level possible and only confirmed species sightings were used in this analysis. Vessel position was recorded on the Garmin 48 global positioning system (GPS) every minute. Environmental data were collected at the turn point of each transect leg and when weather conditions changed. Environmental data included as covariates for analysis were julian day and sea state. Sea state was taken as an average across the legs of each transect. Other variables included number of scientists on board and survey start time, as a proxy for sun glare.

Transect data collected during each transect were downloaded from the GPS and saved as text files. Data collected concurrently on paper sheets were transferred to an access database and were verified by two transcribers.

Analytical methods

Data from each on-effort transect that was completed in a single day between July 2000 and November 2006 were extracted from an Access database. Off-effort tracks, those to the survey start point, from the survey end point to the harbour and those made during encounters, were discarded. Encounters (closing mode) and sightings (passing mode) were extracted. Data were included only where positive species identifications were made by research assistants and scientific observers. Latitude and longitude were converted to decimal degrees for GIS mapping. Macros were run to extract each new encounter and remove repeats. Manual comparison of the database with the written data sheets was then undertaken to check for errors and duplicate and possible duplicate sightings were removed. Possible duplicate sightings included those reported on sightings sheets as such. In addition, those sightings of Blainville's beaked whales made within an hour of each other within the same section of the study area were removed. Photo-identification of individuals was used for confirmation of group identity to aid verification of duplication where possible (Hickmott, pers. comm.).

The standardised methodology enabled sightings data from each transect to be summarised as the total number of whale groups and individuals observed on each completed transect. Environmental and other variables were summarised over each transect. Statistical methods used are shown (Table 2). The counts and environmental data for each separate transect were then viewed as replicates within each year. Both encounters and sightings were investigated for all species.

Table 2. Description of covariates used in analysis of surveys conducted off Great Abaco Island, Bahamas between July 2000 – November 2006; *Some transects completed in BSS3 (described fully under field methods)

Variable	Statistical method used over transect	Range
Julian day	-	001 – 365 d
Sea state	Median/mode	0 – 2*
Number of scientists	Mean	0 – 3
Start time of survey	-	07.00 – 19.00 hr

Initial data exploration was undertaken in Microsoft Excel, where variables were extracted from an access database and plotted to indicate relationships between whale counts and covariates, to detect outliers and errors and to illustrate trends before more formal model-based analysis (McCarthy, 2007).

Model specification

GLMs (McCullagh and Nelder, 1989) were constructed to describe the annual abundance trends in deep diving cetacean species observed during replicate counts (completed transects) and to analyse relationships between counts and covariates. The Poisson univariate distribution is a discrete probability distribution commonly used to represent count data, where data are discrete, non-negative integers. The Poisson GLM is often called the Poisson regression model and assumes that λ is Poisson with mean and variance, μ (Gelman *et al.,* 2003). The Poisson distribution expresses the probability of an independent number of events, in this case individuals counted per transect, x, occurring in a fixed period of time, with known average rate:

$$F(x; \lambda) = e^{-\lambda}\lambda^{x}/x!$$

where:

e = base of the natural logarithm ($e = 2.71828$)

$x!$ = the factorial of x, and

λ = a positive real integer, equal to the expected number of events that occur during the given interval.

The logarithmic link function is typically chosen in Poisson regression, so data were transformed logarithmically to ensure positive counts that could then be related to explanatory covariates in a linear regression:

$$\ln(\lambda_{ti}) = bx_{ti}$$

where:

b = an unknown parameter vector to be estimated, and

x_{ik} = a vector containing information on the state of covariates, describing julian day, sea state, number of scientists on board, survey start time and individual effects of survey year.

Continuous explanatory variables were centred by subtracting their sample mean. This makes them orthogonal to the intercept, reducing correlation between samples and improving efficiency of the Markov Chain Monte Carlo (MCMC) sampling, a standard statistical computation for modern Bayesian methods (McCarthy, 2007; Crainiceanu *et al.,* 2003; described below). Without centring, high autocorrelation between MCMC values can lead to inefficient and possibly unrepresentative sampling of the posterior distribution without large numbers of samples (McCarthy, 2007).

The models were developed for the ith completed transect in year k. This resulted in the following general model:

$$\ln(\lambda_{ik}) = \text{b.year}[k] + \Sigma b x_{ik}$$

where:

b.year[k] = overall level of the counts for each year between 2000 and 2006. The parameter b.year served as the intercept, which was adjusted by the effects of each covariate to give the real count. The intercept parameters could therefore be interpreted on the real (rather than log) scale as an idealised 'annual index', or the count that would be observed on a transect under standard covariate conditions. The b.year[k] parameters were drawn from a Normal random effects prior distribution with an overall mean, mu.b.year, and a standard deviation, sd.b.year. The overall mean, mu.b.year, was assigned a non-informative prior distribution (on the log scale) centered on zero with large standard deviation (=10) to allow the overall mean to be estimated without prior constraints. The prior for the overall standard deviation, sd.b.year, was assigned a Uniform distribution between 0 and 10 to allow individual years to differ from the mean if supported by the data.

Data on each covariate was provided by the term x_{ik}, which was entered into the model through multiplication with a vector of parameters, b, describing the strength of the linear relationship between each covariate and the whale count. Here b.day represented the parameter for the relationship with julian day, b.bss represented sea state, b.scobs was the number of scientists on a transect and b.start was the survey start time (Eq.1; Table 5). Each of the b parameters was assigned a separate (fixed effect) prior distribution, specifically a Normal distribution centred on zero with a large standard deviation of 10 to allow non-zero relationships to emerge. The general model with all covariates was therefore represented below:

$$\log(\mu[i,k]) = \text{b.year}[k] + \text{b.day} + \text{b.bss} + \text{b.scobs} + \text{b.start} \qquad (1)$$

Bayesian Inference: prior to posterior updating

In Bayesian inference, the model links the data to the parameters in what is termed the 'likelihood function' and this is used to update the prior distributions on the parameters to posterior distributions conditional on the observed data (Figure 7; Ellison, 1996). Bayes theorem defines the posterior probability as proportional to the prior probability multiplied by likelihood function (data). Therefore the likelihood modifies the prior, to determine the resulting posterior probability.

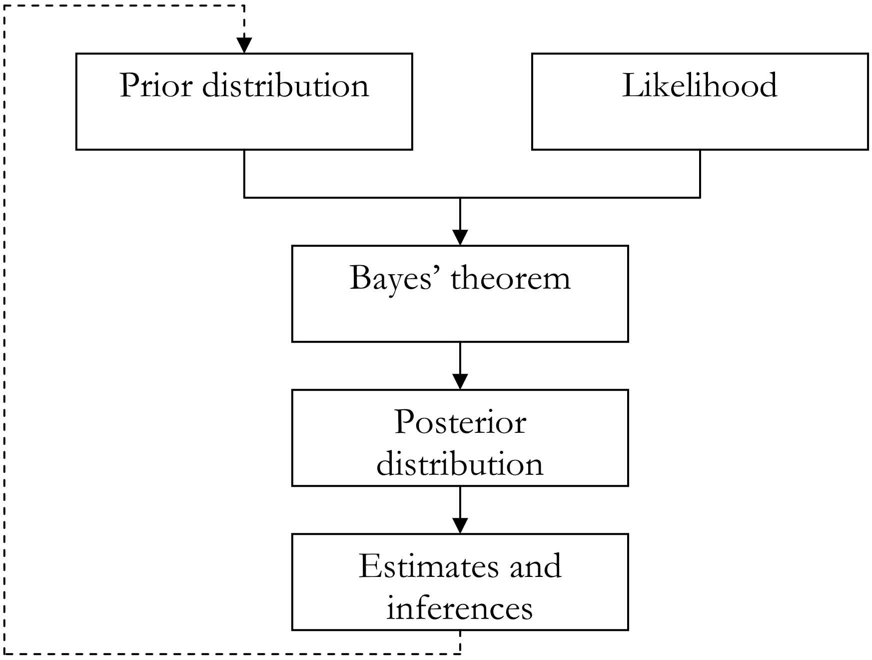

Figure 7. The simplified process of a Bayesian analysis (adapted from Open University, 2007). Dashed line indicates iterative process, as information is gathered.

Bayesian analysis thus provides estimation of parameters as (posterior) probability distributions that summarise uncertainty about the parameter, given the observed data (Fryback *et al.,* 2001). In modern computational statistics, parameter sets are simulated from the priors, and the likelihood is calculated for a series of computer-generated samples from the posterior distribution of interest (Buckland *et al.,* 2004). All that is needed to define the sampling distributions are conditional relationships between individual parameters and the data. WinBUGS software was used to specify the model through object-oriented computer code, assign prior distributions to parameters, set up the sampling distributions and sample from the posterior distributions using MCMC simulation (Lawson *et al.*, 2003).

MCMC draws repeated, but correlated, samples from a posterior distribution. The chain explores the full posterior distribution as the number of samples increases, and converges to the region of highest posterior probability. Therefore, the posterior distribution can be summarised by the proportion of iterations drawn from a particular portion of the parameter space. Gibbs sampling is a common MCMC sampling algorithm used in Bayesian analysis (Gelman and Gelman, 1984) and is the standard updating method used in WinBUGS software. Initial values were set for the start-point of the chain, and then a new value for each parameter was sampled from the corresponding parameter's full conditional distribution at each iteration (Lunn *et al.,* 2000). Initial values can be somewhat arbitrary but convergence to the regions of non-negligible posterior probability can be very slow if inappropriate values are chosen (Lawson *et al.*, 2003). Initial values were therefore based on preliminary MCMC runs to explore the parameter space.

For each dataset and model combination, a three-chain MCMC run was generated to assess convergence of the MCMC routine, and inference was based on 20,000 iterations after convergence was achieved. The length of the 'burn-in' prior to convergence was assessed by visual comparison of the history of each of the chains (Figure 8), and more formally assessed using the method of Gelman and Rubin (1992), as modified by Brooks and Gelman (1998). This is based on summary statistics comparing the variances within and between the three different simulated sequences (applied in WinBUGS). Burn-in was relatively fast for each model, occurring within 10,000 iterations. Simulating 20,000 samples following convergence ensured good mixing of the chains through the range of the posterior density (Fryback *et al.,* 2001).

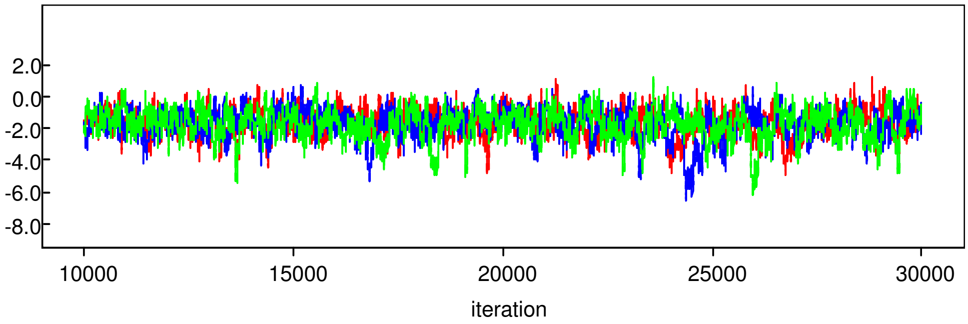

Figure 8. An illustration of convergence of three Markov Chain Monte Carlo (MCMC) chains

Computation of sample statistics (where the default statistics include the mean, median, standard deviation, standard errors, 2.5 and 97.5 quartiles), kernel density plots and sample traces allowed exploration of the posterior distribution. Density plots were examined, using the terms b.bss, b.day, b.scobs and b.start, to determine proportion of the distribution greater than or less than zero for the probability of positive or negative effects. Where a distribution was centered on zero, no effect was supported.

Bayesian credible intervals are the range of parameter values that encompass 95% of the sampled values (or 95% of the posterior density) thus representing a 95% chance that the true value will fall within the interval, providing ecologically meaningful results (McCarthy, 2007). This is a more natural, and different definition than frequentist 95% confidence intervals, which can be difficult to understand and interpret. Credible intervals are wider when the posterior is less precise, therefore providing a concept of power (McCarthy, 2007), and an intuitive measure of support for different parameter values. In this study, counts of species on each transect were investigated to estimate abundance trends between July 2000 and November 2006 incorporating information on the state of covariates determined by the deviance information criteria (DIC). Credible intervals support DIC in assessment of results and were used to determine the statistical power. These can be used to infer biological significance as well as statistical significance (McCarthy and Parris, 2004).

Model diagnostics - deviance information criteria (DIC)

An information theoretic approach using the DIC was used to evaluate the fit of a suite of comparative models for each species (Spiegelhalter *et al.,* 2003). Specifically, investigation of whether all covariates were supported by the data was undertaken, or if an optimal model fit could be obtained using only a subset of the available covariates. DIC is a Bayesian alternative to the AIC (Aikaike's information criteria) often used in standard frequentist approaches (Ellison, 2004). The DIC can be thought of as a means to evaluate trade off between the complexity and explanatory power of the model where high explanatory power is assumed to be good and high complexity is not (Wintle *et al.,* 2005).

The DIC value was calculated for each model on the basis of deviance explained by the model and the number of covariates in the model. The model with the smallest DIC value was selected as the best fitting and hence the most parsimonious model. Models with similar DIC provide a level of support and so a set of plausible models (McCarthy, 2007). A small difference in DIC values has been reported as < 5 (Thogmartin and Knutson, 2007; Golicher *et al.,* 2006) and as 2 or 3 units (Shukuroglou and McCarthy, 2006). A difference of 3 – 7 demonstrates considerably less support and a difference of more than 10 DIC units indicates an inferior model with no support (Spiegelhalter *et al.,* 2002).

Model building

WinBUGS version 1.4 was the freely downloadable software used for model construction and statistical analyses. WinBUGS can be used to construct and fit Bayesian probability models to a range of data, where all quantities are treated as random variables. A WinBUGS file contains all information required to run the analysis: the constructed model, the data to compile the distributions and the initial values, in the text-based BUGS language (Lawson *et al.*, 2003; Appendix A). Field data were transferred and input in list format (e.g. number of years, counts of number of surveys in each year) and array format (in separate txt files) for the individual species counts and other covariate data from Microsoft Excel by copying and pasting through Microsoft Notepad. More details of the steps undertaken to run WinBUGS are available in the User Manual (Spiegelhalter *et al.*, 2003). The step by step process of how WinBUGS was used can be found (Open University, 2007).

Prior distributions on parameters

A non-informative Normal prior distribution was assumed for each unknown parameter (Table 3). Results of Bayesian methods using uninformative priors are equivalent to standard frequentist analysis, with the benefit of more easily incorporating complexity into the models (Shukuroglou and McCarthy, 2006).

Centring on zero with very large variance means that the prior is essentially uniform across the range of data (Ellison, 2004) and hence the data dominates the posterior (McCarthy, 2007). Non-informative normal prior distributions centred on zero were determined for each variable parameter (Table 3). The precision term allowed for non-zero effects to emerge.

Table 3. Prior distributions for model parameters, with distributions specified as Normal(mean, variance)

Parameter	Description of variable	Centred?	Prior distribution
b.year	Overall level of counts for each year	-	Normal(0, 100)
b.bss	Sea state	Y	Normal(0, 100)
b.day	Julian day	Y	Normal(0, 100)
b.scobs	Number of scientific observers	Y	Normal(0, 100)
b.start	Survey start time	Y	Normal(0, 100)

RESULTS

Completed transects

Based on the Bahamas Marine Mammal Research Organisation (BMMRO) survey data, 80 days of completed transects were conducted between July 2000 and November 2006, totalling 1,573.85 nm on survey effort. Fifty eight (58) incomplete transects were discounted due to incomplete coverage of the transect grid. Completion of transects took between 53 m and 2 hr 06 m, with a mean on-effort search time of 1 hr 37 m. Number of completed transects varied annually, between 4 and 22 transects, with fewer transects completed in more recent years (Figure 9). Number of completed transects also varied seasonally, with a minimum of ten between Oct-Dec and a maximum of 25 between Jul-Sept, over the study period (Figure 10).

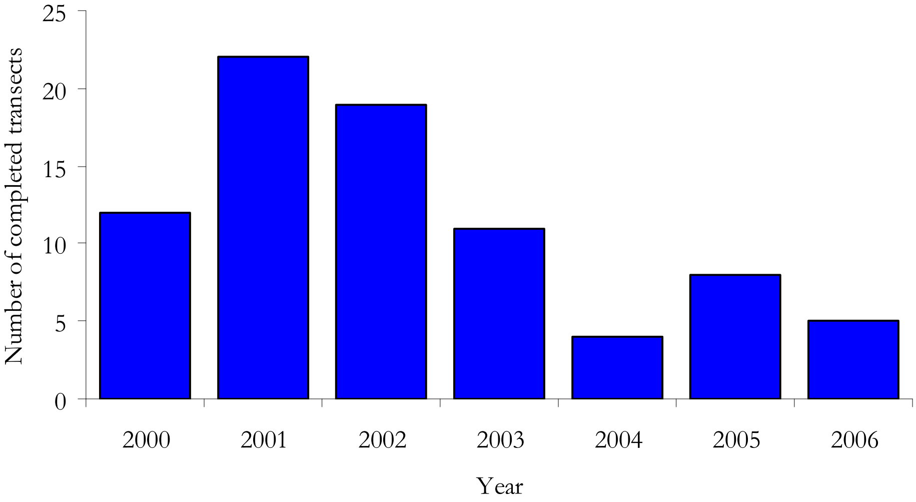

Figure 9. Annual variation in survey effort conducted off Great Abaco Island, Bahamas between July 2000 – November 2006

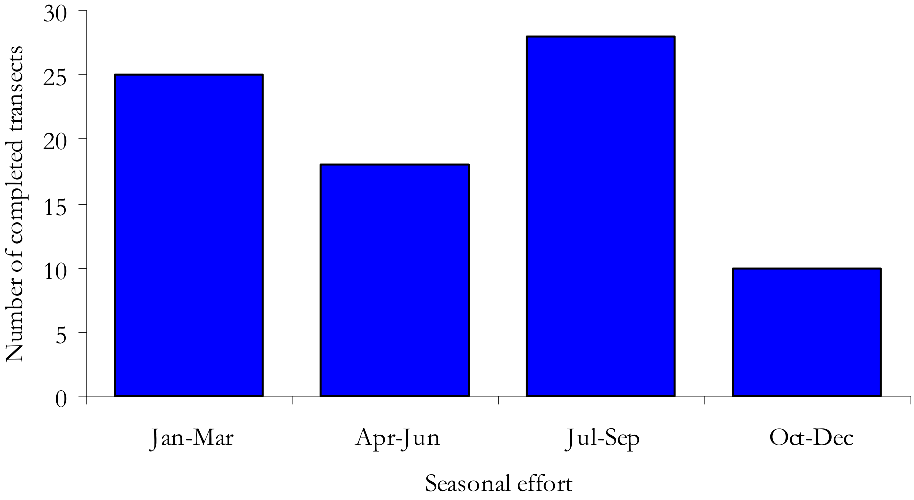

Figure 10. Seasonal variation in survey effort conducted off Great Abaco Island, Bahamas between July 2000 – November 2006

Species observed

Nine species, consisting of 101 groups (and 568 individuals), were positively identified on completed transects during the study period. Number of groups and individuals observed, percentage of encounters of each species and encounter rates varied (Table 4). Dwarf sperm whales, Blainville's beaked whales, bottlenose dolphins and sperm whales were the most frequently sighted species in the study area (Table 4; Claridge, 2006) whilst bottlenose dolphins and Atlantic spotted dolphins (*Stenella frontalis*) occurred in the largest groups. Number of groups observed on effort is shown (Figure 11).

Table 4. Groups of cetacean species, individuals, percentage of groups seen and mean encounter rates (average per transect) on completed transects conducted off Great Abaco Island, Bahamas between July 2000 – November 2006

Species	**No. of groups (individuals)**	**Percentage of total groups (%)**	**Mean encounter rate (per km)**	
			Groups	**Individuals**
Dwarf sperm whale (*Kogia sima,* Ks)	42 (140)	42	0.0273	0.0913
Blainville's beaked whale (*Mesoplodon densirostris,* Md)	21 (105)	21	0.0137	0.0685
Bottlenose dolphin (*Tursiops truncatus,* Tt)	11 (144)	11	0.0078	0.0949
Sperm whale (*Physeter macrocephalus,* Pm)	10 (55)	10	0.0065	0.0358
Atlantic spotted dolphin (*Stenella frontalis,* Sf)	7 (81)	7	0.0046	0.0530
Pygmy sperm whale (*Kogia breviceps,* Kb)	4 (7)	4	0.0026	0.0046
Cuvier's beaked whale (*Ziphius cavirostris,* Zc)	3 (6)	3	0.0020	0.0039
Pantropical spotted dolphin (*Stenella attenuata,* Sa)	2 (32)	2	0.0013	0.0207
Long-finned pilot whale (*Globicephalus melas,* Gm)	1 (3)	1	0.0007	0.0020
Total	101 (568)			

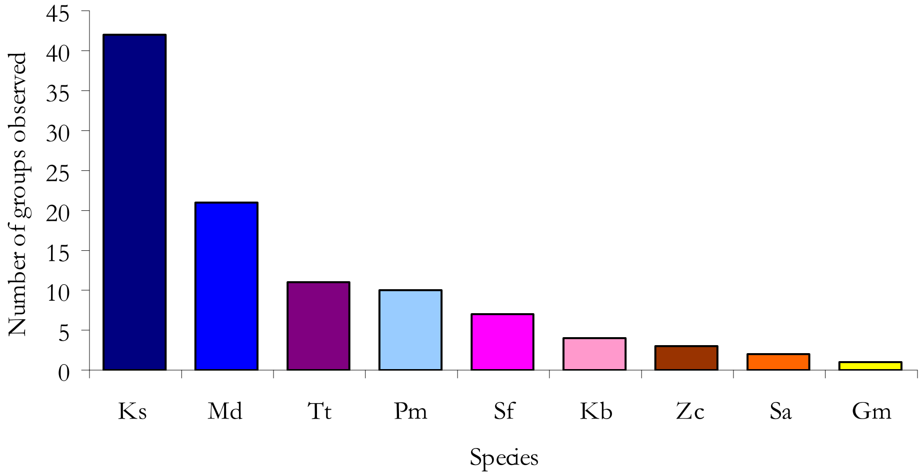

Figure 11. Cetaceans species observed in the study area on-effort during completed transects between July 2000 – November 2006

Not surprisingly, the number of cetacean groups encountered per year varied in relation to the number of completed transects during each survey year (Figure 12). With the exception of the first survey year in 2000, where most dwarf sperm whales and Blainville's beaked whales were encountered despite more effort in 2001, and low Blainville's beaked whales in 2001 despite the highest effort, a general trend can be detected whereby sightings rates increased for all species with increasing frequency of surveys.

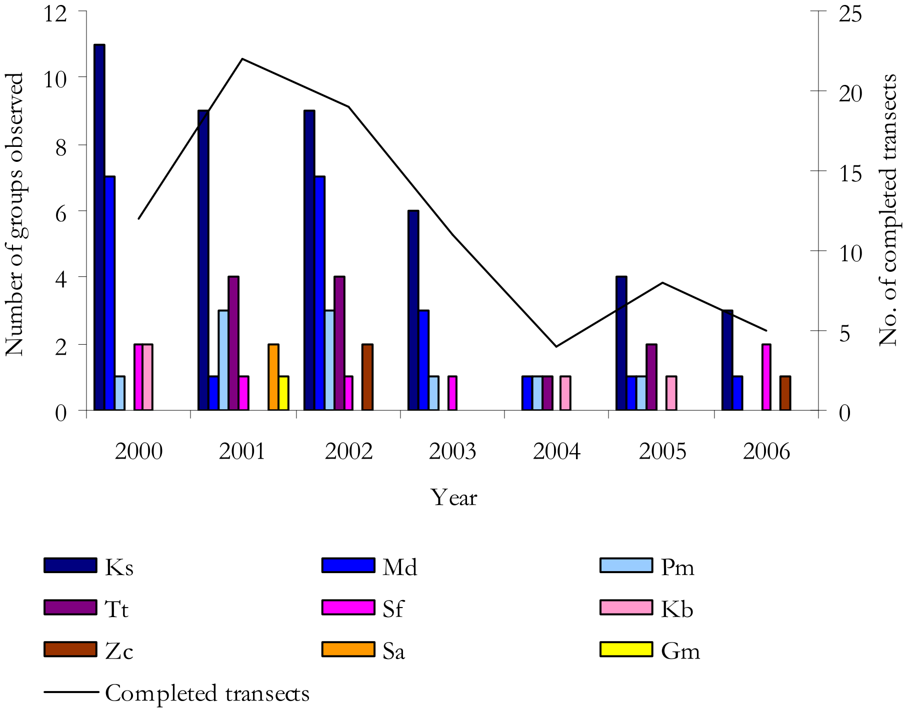

Figure 12. Groups of study species encountered per year during completed surveys off Great Abaco Island, Bahamas between July 2000 – November 2006

Study species

Dwarf sperm whales, Blainville's beaked whales and sperm whales were encountered on 42, 21, and 10 occasions respectively during 80 completed transects. Group size varied (dwarf sperm whales: 1-23; Blainville's beaked whales: 1-8; Sperm whales: 1-8).

Covariates

Before fitting the statistical models, possible relationships between encounters of dwarf sperm whales, Blainville's beaked whales and sperm whales and covariates: julian day, sea state, number of scientists and survey start time, were investigated. Blainville's beaked whales were observed in every year, dwarf sperm whales were not observed in 2004 and sperm whales were not observed in 2006. Sightings were spread throughout the different months, although not all species were observed in every month (Figure 13). There was a peak in Blainville's beaked whale observations in August and a peak in Dwarf sperm whale observations in October. Nine of the ten sperm whale observations in the study area were made between January and July, with an outlying observation in November. No observations were made in December, when only one transect was completed during the study period.

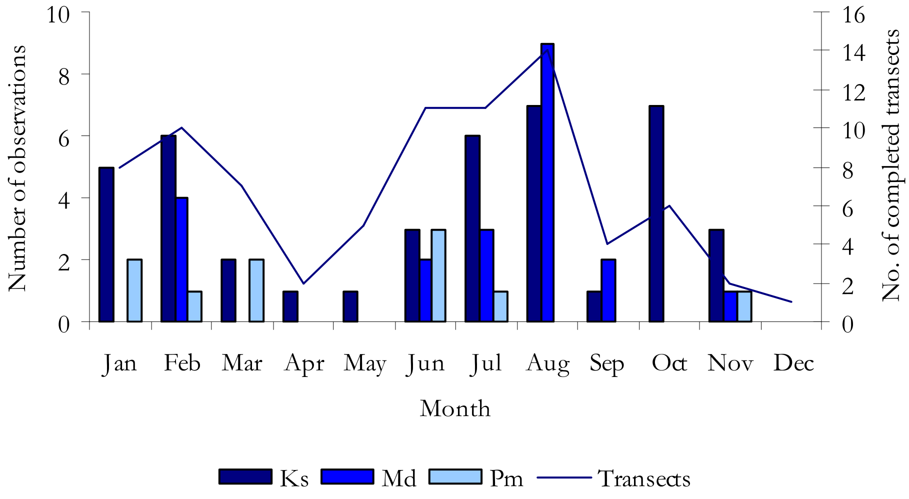

Figure 13. Groups of dwarf sperm whales, Blainville's beaked whales and sperm whales encountered per month during surveys off Great Abaco Island, Bahamas between July 2000 – November 2006

As expected, observations of dwarf sperm whales and Blainville's beaked whales decreased with increasing sea state, the relationship with sperm whales is not so clear (Figure 14).

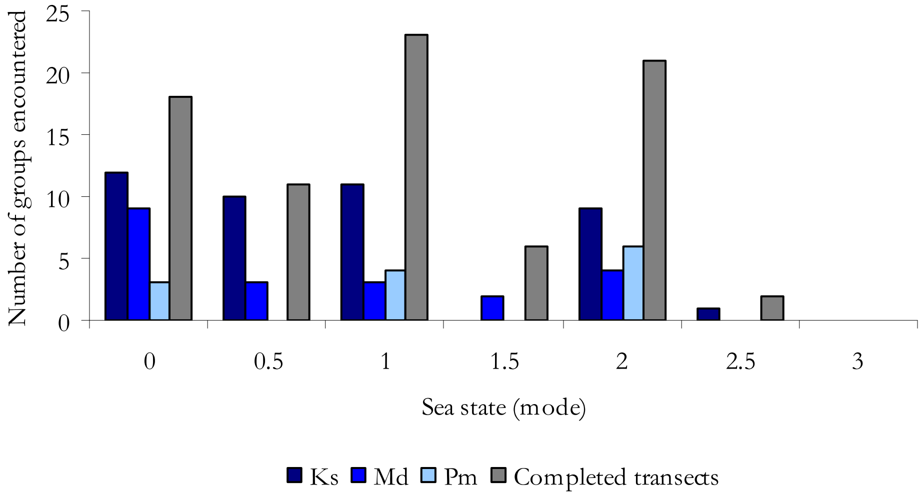

Figure 14. Observations of dwarf sperm whales, Blainville's beaked whales and sperm whales in relation to sea state during surveys off Great Abaco Island, Bahamas between July 2000 – November 2006

No observations were made when there were no scientific observers on board. The observation rate showed no clear pattern with increasing number of scientific observers (Figure 15). Group encounter rate per transect varied from 3.56, 2.34 and 3.17 with one, two or three scientific observers on board respectively (mean encounter rate, 2.26).

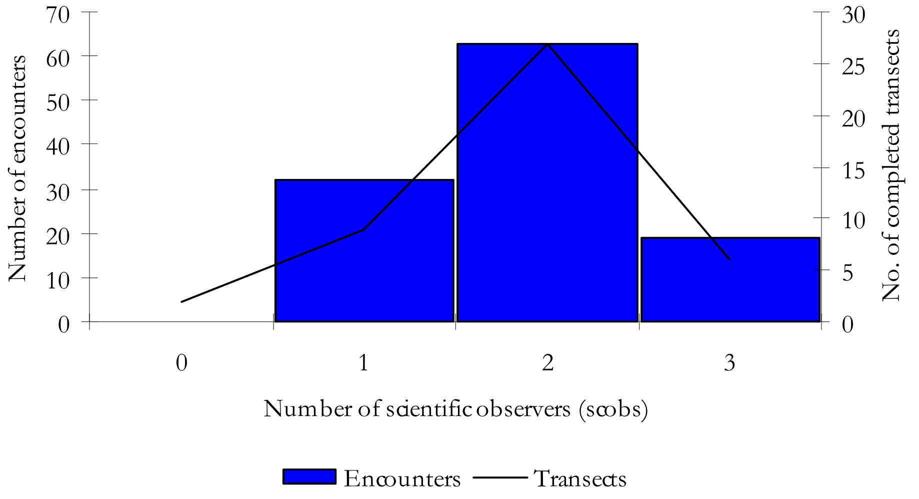

Figure 15. Observations of dwarf sperm whales, Blainville's beaked whales and sperm whales in relation to number of scientific observers during surveys off Great Abaco Island, Bahamas between July 2000 – November 2006

Survey start time varied from 07:11 to 17:16 hours. However, 47.5% of completed transect surveys were started before 11:00 (Figure 16).

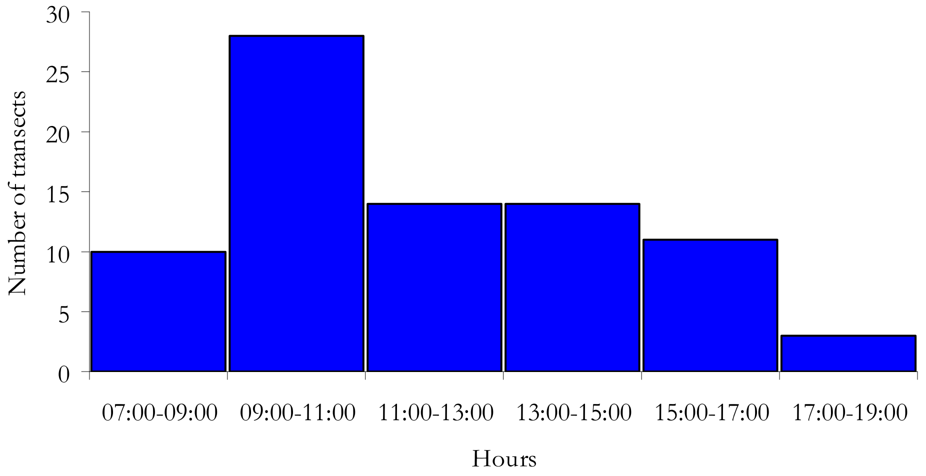

Figure 16. Histogram of the survey start time of completed transects during surveys off Great Abaco Island, Bahamas between July 2000 – November 2006

Generalised linear model (GLM)

Thirteen models were fitted to the datasets for dwarf sperm whales, Blainville's beaked whales and sperm whales respectively, using the Bayesian software WinBUGS. The DIC value for the general model, including all covariates: year, julian day, sea state, number of scientists on board and survey start time, was within five DIC units of the model with the best fitting DIC for dwarf sperm whales and Blainville's beaked whales and within one unit of the best fitting DIC for sperm whales (Table 5). All models were within about six units of the model providing the best fit to the sperm whale data. There was a clear divide between those models that provided a fit within five DIC units of the best fitting model for both dwarf sperm whales and Blainville's beaked whales, and then a step in DIC units to those models that were > ten DIC units from the best fitting model, indicating the inferiority of some models, with essentially no support. For both dwarf sperm whales and Blainville's beaked whales, the poorly fitting models did not include the covariates that were in the model providing the lowest DIC and hence the best fit, which was reassuring.

Table 5. Bayesian deviance information criteria (DIC) used to identify generalised linear model (GLM) that best fitted the data. Lowest DIC values for each species in bold; *DIC for GLM including all covariates; ΔDIC is the difference between the best model and the model of interest

Species	Model	DIC	ΔDIC
Dwarf sperm whale, *Kogia sima*			
	day, bss	**391.536**	0
	day, bss, start	393.495	1.959
	day, bss, scobs	393.519	1.983
	day, bss, scobs, start	*395.455	3.919
	bss	406.137	14.601
	bss, start	407.187	15.651
	day	407.377	15.841
	bss, scobs	408.435	16.899
	day, scobs	408.457	16.921
	day, start	409.473	17.937
	start	419.248	27.712
	scobs	419.403	27.867
	start, scobs	421.142	29.606
Blainville's beaked whale, *Mesoplodon densirostris*			
	bss	**311.355**	0
	bss, start	312.455	1.100
	day, bss	312.720	1.365
	bss, scobs	313.287	1.932
	day, bss, start	313.998	2.643
	day, bss, scobs,	314.568	3.213
	day, bss, scobs, start	*315.888	4.533
	start	330.594	19.239
	day	331.972	20.617
	scobs, start	332.118	20.821
	Day, start	332.176	20.763
	scobs	332.271	20.916
	day, scobs	333.875	22.520
Sperm whale, *Physeter macrocephalus*			
	scobs, start	**268.968**	0
	scobs	269.728	0.760
	day	269.971	1.003
	bss, scobs	269.990	1.022
	day, bss, scobs	270.125	1.157
	day, scobs	270.221	1.253
	day, bss, scobs, start	*270.376	1.408
	day, bss	270.399	1.431
	day, start	270.758	1.790
	day, bss, start	271.345	2.377
	start	272.578	3.610
	bss, start	274.231	5.263
	bss	275.009	6.041

GLM including all covariates

Density plots of posterior distributions for each species, initially using the model incorporating all the covariates, are shown (Figures 17 - 19). Density plots of the covariates were not skewed but the median values obtained were investigated rather than the mean to provide a more robust representation of the data. Dwarf sperm whales provided evidence for a negative relationship between counts and sea state (b.bss), and a weak but significant negative relationship between counts and julian day (b.day). The significance of these relationships is observed in the posterior distributions which do not overlap with zero, resulting in a 100% probability that they are less than zero. Both number of scientists on board (b.scobs) and survey start time (b.start) are centred around zero and therefore had a negligible effect on counts (Figure 17). Distributions of the b parameters are unimodal and are not skewed.

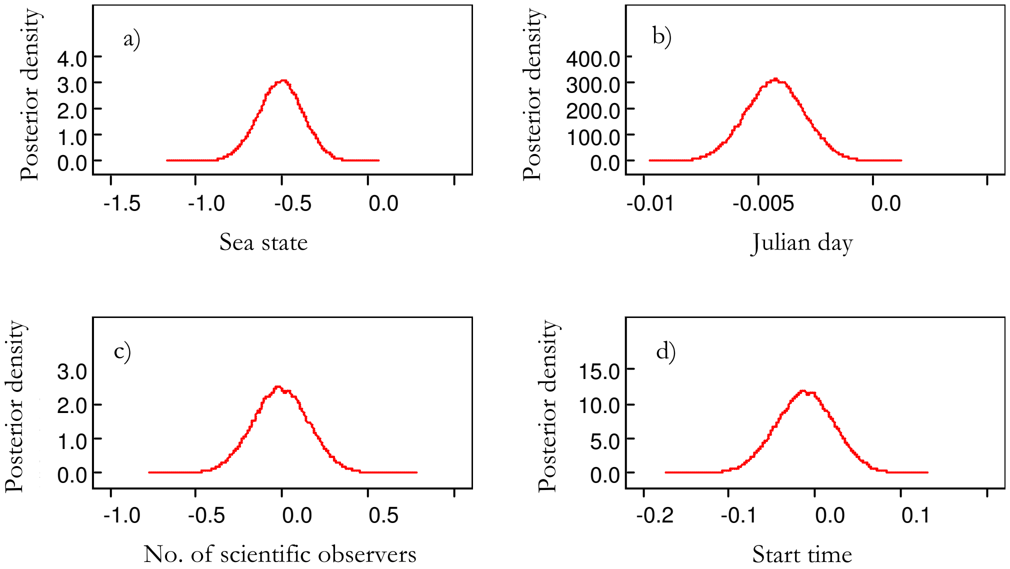

Figure 17. Dwarf sperm whale density plots of posterior distribution for the model including all covariates: a) sea state, b) julian day, c) scientific observers and, d) survey start time

Blainville's beaked whales provided strong evidence for a negative relationship between counts and sea state (b.bss), and a weak positive relationship between counts and number of scientific observers (b.scobs). Both julian day (b.day) and survey start time (b.start) are centred around zero and had a negligible effect on estimates (Figure 18). Distributions of the b parameters are unimodal and are not skewed.

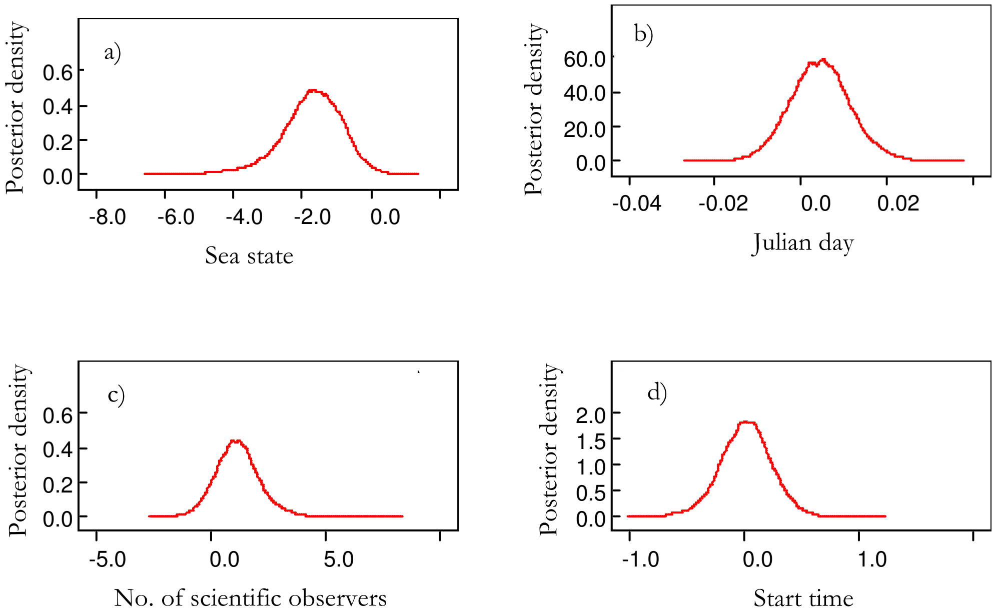

Figure 18. Blainville's beaked whale density plots of posterior distribution for the model including all covariates: a) sea state, b) julian day, c) scientific observers and, d) survey start time

Sperm whales provided evidence for a positive relationship between counts and number of scientific observers (b.scobs), and a weak negative relationship between counts and bss (b.bss), start (b.start) and a very weak relationship with day (b.day) (Figure 19). Distributions of the b parameters are unimodal and are not skewed.

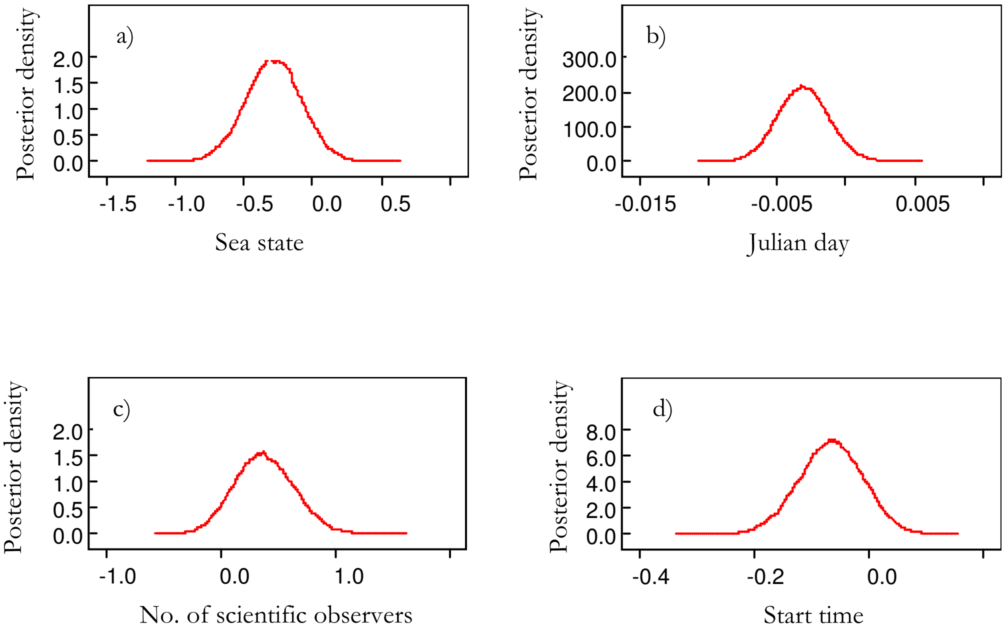

Figure 19. Sperm whale density plots of posterior distribution for the model including all covariates: a) sea state, b) julian day, c) scientific observers and, d) survey start time

These relationships mirror the results of the model DIC selection, with strong effects re-occurring for the parameters that were included in the best-fitting models that are detailed in the next section.

The standardised annual index represents the idealised number of animals expected per survey once account has been taken of other covariates. Box plots of annual estimates for each species indicated the same trends regardless of covariates in the model. The credible intervals surrounding annual estimates for each species did not contain zeros. Results of the models that demonstrated the best fit of the data for each species are presented below.

Optimum model for each study species

Dwarf sperm whale

Covariates

The WinBUGS program for the best fitting dwarf sperm whale model is provided in BUGS programming language (Appendix A). The model that provided the best fit to the data for dwarf sperm whales included julian day and sea state (Eq. 2). This model fit the data better that the next best fitting model by almost two DIC values (Table 5). Day and sea state were represented in five models that provided the lowest DIC values and hence provided the best fit to the data. Summary statistics of the best fitting model are provided (Table 6).

$$\log(\mu[i,k]) = \text{b.year}[k] + \text{b.day} + \text{b.bss} \qquad (2)$$

Table 6. Summary statistics of posterior means and percentiles from WinBUGS analysis of best fitting model for dwarf sperm whale abundance estimates, including julian day and sea state, off southwest Great Abaco Island, Bahamas between July 2000 – November 2006

node	mean	sd	MC error	2.50%	median	97.50%
annual.index[1]	3.798	0.7721	0.004293	2.447	3.742	5.468
annual.index[2]	1.281	0.2349	0.001121	0.8636	1.267	1.779
annual.index[3]	1.168	0.2329	0.001256	0.7592	1.151	1.67
annual.index[4]	1.606	0.3598	0.001558	0.9826	1.577	2.39
annual.index[5]	0.2291	0.209	0.0019	0.003354	0.1717	0.7693
annual.index[6]	1.231	0.3957	0.001707	0.5864	1.188	2.128
annual.index[7]	1.242	0.474	0.001942	0.4971	1.181	2.336
b.bss	-0.5065	0.1279	6.63E-04	-0.7586	-0.5064	-0.2595
b.day	-0.00434	0.001234	7.53E-06	-0.00678	-0.00432	-0.00194
b.year[1]	1.314	0.2045	0.001161	0.895	1.32	1.699
b.year[2]	0.2309	0.1847	8.87E-04	-0.1467	0.2367	0.5759
b.year[3]	0.1356	0.2009	0.001084	-0.2755	0.1407	0.5125
b.year[4]	0.4486	0.2263	9.80E-04	-0.01754	0.4554	0.8715
b.year[5]	-2.059	1.459	0.01384	-5.698	-1.762	-0.2623
b.year[6]	0.1557	0.328	0.001414	-0.5338	0.172	0.755
b.year[7]	0.1424	0.3937	0.001604	-0.6989	0.1667	0.8485
mu.b.year	0.05232	0.6553	0.00355	-1.418	0.1103	1.195
prob.bss	6.67E-05	0.008164	3.32E-05	0	0	0
prob.day	1.33E-04	0.01155	4.67E-05	0	0	0
sd.b.year	1.39	0.8955	0.009399	0.4534	1.156	3.741

There was a negative relationship between dwarf sperm whale counts and sea state, indicating that observations decreased as sea state increased (Figure 20). Estimates and julian day showed a weak negative relationship, indicating that observations decreased throughout the year. Start and scobs both intercepted zero at about the mid-point of the density distribution and thus demonstrated a negligible effect on estimates, with the use of a GLM.

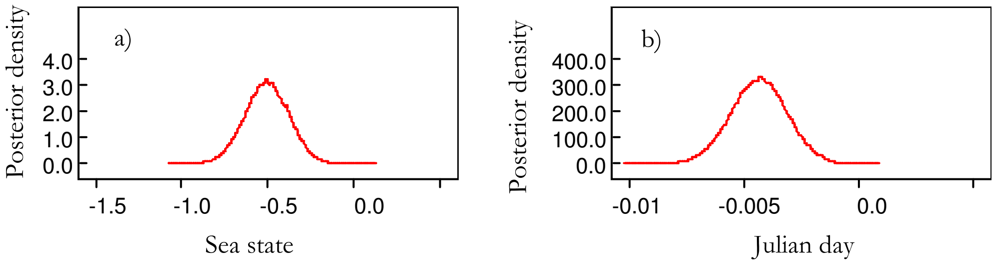

Figure 20. Dwarf sperm whale density plots of posterior distribution for the best fitting model including: a) sea state and b) julian day off southwest Great Abaco Island, Bahamas between July 2000 – November 2006

Abundance trends

Dwarf sperm whale abundance estimate was highest during 2000 and lowest in 2005 (Figure 21). The estimate fluctuated from year to year and a general negative trend was observed overall. However, much of this downward trend was due to a relatively high estimate in 2000. Credibility intervals surrounding the annual index were wide in the first and last year of all dwarf sperm whale models indicating low statistical power and therefore some uncertainty about the data. However, the intervals for 2000 do not overlap with the following years, indicating a significant drop in abundance in survey years following 2000.

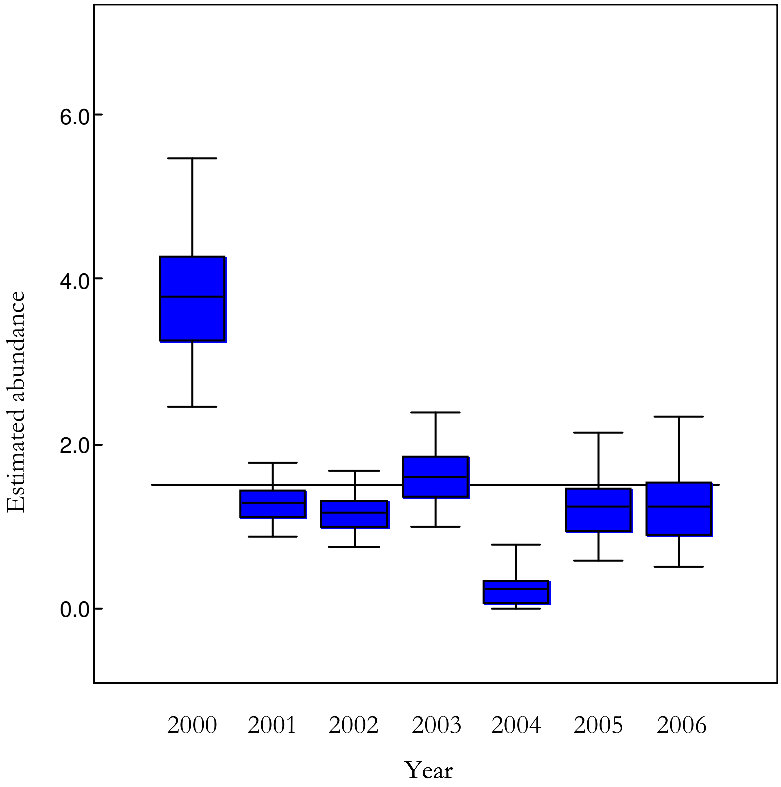

Figure 21. Bayesian estimate of annual dwarf sperm whale abundance estimates, demonstrated by the annual effect b.year[k], and incorporating the effect of julian day and sea state from July 2000 – November 2006 (bars represent the median, quartiles and 95% credibility intervals from the posterior distribution)

Blainville's beaked whale

Covariates

Based on the calculated DIC values, the model that provided the best fit to the data for Blainville's beaked whales included sea state (Eq. 3). The DIC for the five models that best fit the data were within two units of the best fitting model, suggesting a similar level of fit, and each of these models included sea state with additional covariates (Table 5). Sea state was represented in all of the five models that provided the lowest DIC values and hence provided the best fit to the data, each of which was within two DIC value of the model that best fit the data. Summary statistics of the best fitting model are provided (Table 7).

$$\log(\mu[i,k]) = b.year[k] + b.bss \qquad (3)$$

Table 7. Summary statistics of posterior means and percentiles from WinBUGS analysis of best fitting model for Blainville's beaked whale abundance estimate, including sea state, off southwest Great Abaco Island, Bahamas between July 2000 – November 2006

node	mean	sd	MC error	2.50%	median	97.50%
annual.index[1]	3.652	0.5767	0.002602	2.606	3.62	4.862
annual.index[2]	0.3771	0.1283	6.23E-04	0.1684	0.3629	0.6649
annual.index[3]	1.248	0.2399	0.001079	0.8273	1.232	1.767
annual.index[4]	0.7858	0.2382	0.001093	0.3931	0.7602	1.319
annual.index[5]	0.9374	0.3836	0.001678	0.3553	0.8824	1.837
annual.index[6]	0.6211	0.2641	0.001191	0.2164	0.5845	1.238
annual.index[7]	1.176	0.4507	0.00191	0.4757	1.115	2.23
b.bss	-0.6264	0.1397	6.87E-04	-0.9044	-0.6252	-0.3559
b.year[1]	1.283	0.159	7.16E-04	0.9578	1.286	1.581
b.year[2]	-1.035	0.3516	0.001728	-1.782	-1.014	-0.4081
b.year[3]	0.2034	0.1931	8.71E-04	-0.1896	0.2082	0.5693
b.year[4]	-0.2874	0.3086	0.001397	-0.9336	-0.2742	0.2769
b.year[5]	-0.1487	0.4196	0.00184	-1.035	-0.1251	0.6079
b.year[6]	-0.5695	0.4459	0.002068	-1.531	-0.537	0.2136
b.year[7]	0.08861	0.392	0.001662	-0.7429	0.1085	0.8022
mu.b.year	-0.06719	0.4437	0.002051	-0.9747	-0.05735	0.798
prob.bss	0	0	2.36E-13	0	0	0
sd.b.year	1.024	0.4531	0.003483	0.4898	0.9216	2.171

As with dwarf sperm whales, a negative relationship was demonstrated between Blainville's beaked whales counts and sea state (Figure 22), indicating that observations decreased as sea state increased. Some models indicated a positive relationship between the estimates and the number of scientific observers. Day and start both intercepted zero and thus demonstrated a negligible effect on estimates, with the use of a GLM.

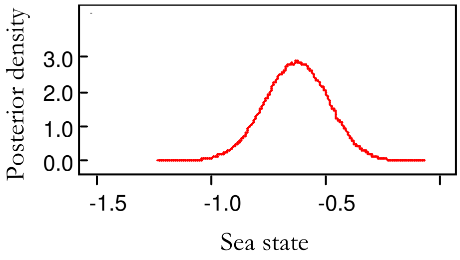

Figure 22. Blainville's beaked whale density plots of posterior distribution for the best fitting model including sea state, off southwest Great Abaco Island, Bahamas between July 2000 – November 2006

Abundance trends

As with dwarf sperm whales, the highest abundance estimate for Blainville's beaked whales was obtained during 2000, with a drop in abundance in each of the following years (Figure 23). The lowest estimate was observed in 2001, and there is no apparent trend between 2001 and 2006.

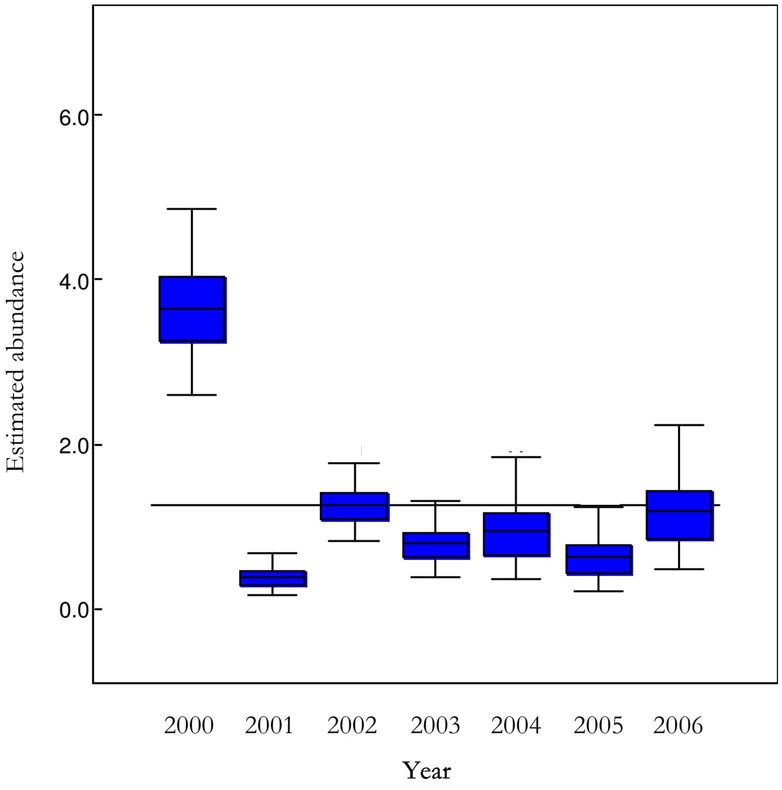

Figure 23. Bayesian estimate of annual Blainville's beaked whale abundance estimates; incorporating the effect of sea state between July 2000 – November 2006 (bars represent the median, quartiles and 95% credibility intervals from the posterior distribution)

Sperm Whale

Covariates

The model that provided the best fit to the data for sperm whales included scientific observers (Eq. 4). The DIC for the nine models that best fit the data were within two units of the model with the lowest DIC value, suggesting a similar level of fit. Not all of these models included scobs (Table 5). The covariates: scientific observers, julian day and sea state appeared in the five models that provided the best fit (Table 5). Summary statistics of the best fitting model are provided (Table 8).

$$\log(\mu[i,k]) = b.year[k] + b.scobs \tag{4}$$

Table 8. Summary statistics of posterior means and percentiles from WinBUGS analysis of best fitting model for sperm whale abundance estimates, including number of scientific observers, off southwest Great Abaco Island, Bahamas between July 2000 – November 2006

node	mean	sd	MC error	2.50%	median	97.50%
annual.index[1]	0.3203	0.1569	0.00177	0.09291	0.2923	0.6952
annual.index[2]	0.7669	0.1753	8.36E-04	0.4645	0.7518	1.151
annual.index[3]	0.9136	0.2345	0.001446	0.5263	0.8887	1.434
annual.index[4]	0.4007	0.171	0.001625	0.1366	0.3767	0.7872
annual.index[5]	1.218	0.5266	0.003549	0.4775	1.122	2.477
annual.index[6]	1.06	0.4764	0.003139	0.4115	0.9622	2.228
annual.index[7]	0.2677	0.2088	0.002452	0.00823	0.2191	0.7636
b.scobs	0.4154	0.2296	0.001934	-0.03458	0.4149	0.8637
b.year[1]	-1.263	0.5183	0.005178	-2.376	-1.23	-0.3636
b.year[2]	-0.2916	0.2306	0.001122	-0.7669	-0.2853	0.1406
b.year[3]	-0.1231	0.2571	0.001608	-0.6418	-0.118	0.3608
b.year[4]	-1.01	0.4518	0.003995	-1.991	-0.9763	-0.2393
b.year[5]	0.1075	0.4289	0.002962	-0.7391	0.1147	0.9071
b.year[6]	-0.03555	0.4354	0.00287	-0.888	-0.03852	0.8011
b.year[7]	-1.767	1.227	0.01295	-4.8	-1.518	-0.2697
mu.b.year	-0.6252	0.5427	0.003231	-1.846	-0.5717	0.3075
prob.scobs	0.9651	0.1835	0.001115	0	1	1
sd.b.year	1.071	0.7413	0.008964	0.1811	0.9075	2.966

A positive relationship between the counts and the number of scientific observers was identified (Figure 24), indicating an increase in observations with increasing number of scientists on board. A weak negative relationship was identified between the counts and julian day. A weak negative relationship was also identified between estimate and sea state, although sea state and start both intercepted zero and thus demonstrated a negligible effect on estimates, with the use of a GLM.

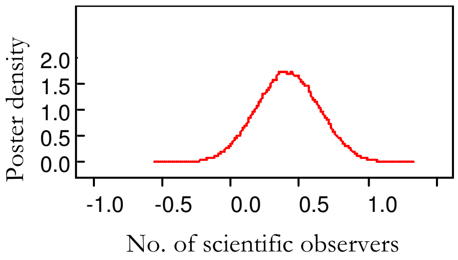

Figure 24. Sperm whale density plots of posterior distribution for the best fitting model including scientific observers, off southwest Great Abaco Island, Bahamas from July 2000 – November 2006

Abundance trends

Variability in abundance estimates of sperm whales across years followed a different pattern to those of dwarf sperm whales and Blainville's beaked whales, where higher estimates for dwarf sperm whales and Blainville's beaked whales corresponded with lower sperm whale estimates (Figure 25). Overall, as expected, abundance estimates were lowest for sperm whales. Available data set was small, and as a result credible intervals were relatively wide, particularly in 2004-2005, indicating low statistical power and therefore some uncertainty about the data (Figure 25; Shukuroglou and McCarthy, 2006).

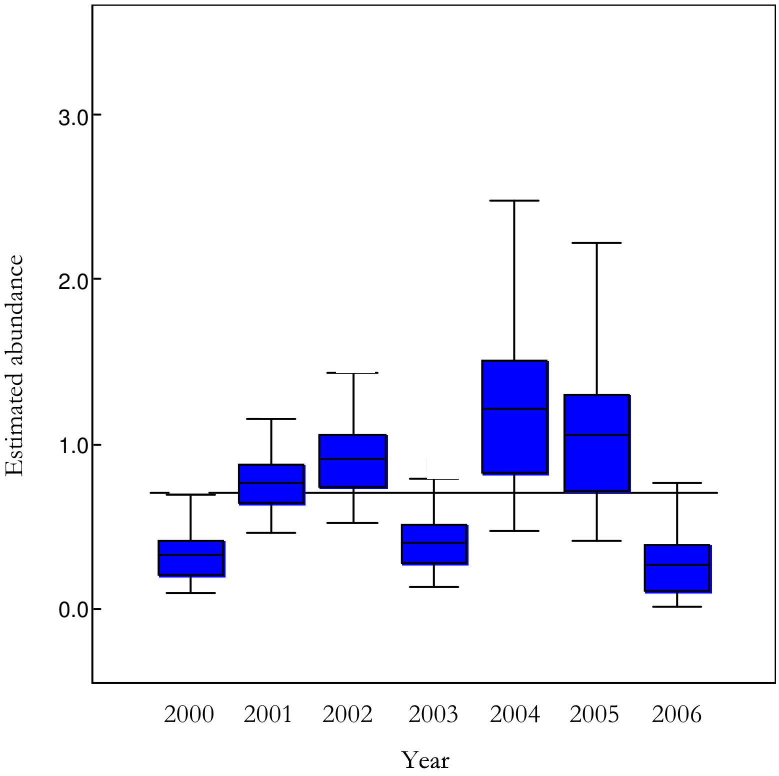

Figure 25. Bayesian estimate of annual sperm whale abundance estimates, incorporating the effect of number of scientific observers between July 2000 - November 2006 (bars represent the median, quartiles and 95% credibility intervals from the posterior distribution)

DISCUSSION

Covariates

Optimal covariates for each model varied between study species. Sea state was an important predictor for both dwarf sperm whale and Blainville's beaked whale abundance estimates. This result is not surprising given the elusive surface behaviour of these two species. A reduction in encounters with both dwarf sperm whales and Blainville's beaked whales with increasing sea state has previously been demonstrated in the study area (Dunphy-Daly, in press; Claridge, 2006). A similar relationship, although weaker, was demonstrated for sperm whales, as expected, given the distinctive visual cue provided by a sperm whale blow. These results further support the negative and often linear effects of increasing sea state that are well documented in the literature. A negative fit with sea state has been identified in studies of *Kogia* in Hawaiian waters (Baird, 2005), Cuvier's and *Mesoplodon* beaked whales in eastern tropical Pacific (Ferguson *et al.,* 2006), harbour porpoises off California (*phocoena phocoena*) (Forney, 1999; 1995) and all species observed on US ship surveys covering different geographic areas (Barlow, 2006; Barlow *et al.,* 2001). The results of this study therefore support previous studies and substantiate efforts to restrict surveys of deep diving species to optimal sea conditions.

Julian day displayed a weak negative relationship with abundance estimates of both dwarf sperm whales and sperm whales suggesting seasonal encounters with these species. Onshore-offshore movements have been previously hypothesised (Ross, 1984), yet only recently has seasonal variation in group size and habitat use of dwarf sperm whales, and a seasonal onshore-offshore movement been demonstrated in the study site (Dunphy-Daly, in press) (although dwarf sperm whales are encountered throughout the year). Nine of the ten sperm whale sightings in the study area were made between January and July, with an outlying observation in November 2000. The seasonal variation in the abundance of female and immature sperm whales reported globally has been related to seasonally abundant food supplies, with home ranges in the order of 1,000 km's not being unusual (Whitehead, 2003). In contrast to the seasonal nature of encounters of dwarf sperm whales and sperm whales, no evidence was provided for seasonal movements of Blainville's beaked whales. Residency has been previously identified in the study area (Claridge, 2006) and off the Big Island in

Hawaii (Sweeney *et al.,* 2007). Confirmation that Blainville's beaked whales remain in the study area year round, whilst dwarf sperm whales and sperm whales undertake seasonal movements, requires further investigation, perhaps with more complex non-linear models. It is difficult to link the movements of any specialist deep diving cetaceans within the study area to seasonal variations in productivity, and hence movement of prey species, as no such investigative work on prey has been conducted in the region to date.

Sperm whale observations increased with an increasing number of scientific observers on the vessel. Perhaps surprisingly, the number of scientists on board showed a negligible effect on dwarf sperm whale and Blainville's beaked whale abundance estimates.

Abundance trends

A clear decrease in abundance estimates of dwarf sperm whales and Blainville's beaked whales was identified after the first year of survey effort. Despite the maximum number of surveys being conducted in 2001, the corresponding abundance estimates of Blainville's beaked whales and dwarf sperm whales during this year were considerably reduced. Estimates for each subsequent survey year continued to be below the estimates in the first survey year. This is in contrast to previous analysis using data collected in the study area that has included opportunistic as well as effort-based data. Sighting rates for Blainville's beaked whales initially declined following the mass stranding event in March 2000 and then increased in 2001 (Claridge, 2006) using a data-set from 1997-2002. Sightings rates of dwarf sperm whales were not found to vary significantly from 2000-2006 (Dunphy-Daly *et al.,* in press). Claridge's study took place in the study area, but included opportunistic sightings that were made during off-effort surveys, whilst the current study was restricted to data collected whilst on-effort. Opportunistic studies resulted in 89% of all observations between 1997 and 2002 (Claridge, 2006) and so could be expected to have a considerable influence over the results where included. Further investigation of effort-based versus opportunistic observations in the study area is therefore required. No trends in abundance data are yet available from other study sites for dwarf sperm whales or Blainville's beaked whales, although these species have been the focus of island-based field studies in other parts of the world (for example, Big Island, Hawaii: McSweeney *et al.,* 2007; El Hierro, Canary Islands: Aguilar Soto, 2006; Tenerife and La Palma, Canary Islands: Tejedor and Carillo, 2006;

Andros Island, Bahamas: Moretti *et al.,* 2006; Madeira archipelago: Freitas *et al.,* 2006; Maldives: Anderson, 2005; east Great Abaco Island, Bahamas: MacLeod *et al.*, 2004; Azores: Silva *et al.,* 2003; La Gomera, Canary Islands: Ritter, 2001).

Annual sperm whale abundance estimates in the study area were consistently low, and confidence intervals overlapped for most years. Nonetheless there does appear to be some variability, with higher estimates in the middle of the time series. Trends in sperm whale populations off the Galápagos Islands were investigated and provided an interesting shift in distribution that could only be elucidated with concurrent broader regional surveys. When females and juveniles in the Galápagos Islands study area became scarce after several years of study, it became apparent that they had shifted to the waters of mainland Ecuador, where previous whaling operations had removed all animals (Whitehead, 2003). Given the broad scale movements of sperm whales across thousands of nautical miles and the relatively small size of this Bahamian study area (encompassing 126nm^2), concurrent broader regional surveys would be worthwhile.

The relationship between the abundance estimates of the three study species is complex. A similar trend in the estimates of dwarf sperm whales and Blainville's beaked whales coincided with an opposing trend (but with a low estimate) for sperm whales. We might expect that dwarf sperm whales and Blainville's beaked whales are more restricted in their range and so in years of lower productivity, sperm whales can cover a broader area in search of prey resource.

Dwarf sperm whales were found to be evenly distributed through the study area and Blainville's beaked whales were found inshore of sperm whales, which were concentrated around 1,000 m depth contour (Claridge, 2006). Off east Abaco Island, habitat segregation has been suggested (Claridge, 2006; MacLeod and Zuur, 2005) with Cuvier's beaked whales in deeper waters than Blainville's beaked whales, and dwarf sperm whales in shallower waters still (Claridge, 2006; MacLeod *et al.,* 2004). However, dwarf sperm whales, Blainville's beaked whales and sperm whales clearly broadly coexist in the study area and this deep diving cetacean community share a trophic level of 4.3-4.4 (Pauly *et al.,* 1998). Niche partitioning between deep diving cetaceans has been discussed in a number of studies (Claridge, 2006;

Hickmott, 2005; Whitehead and MacLeod, 2003). Within a particular region, differences in cephalopod prey by size (and hence depth) and species causes a partitioning so that different species are not in direct competition (Waring *et al.,* 2001; Clarke, 1996). Based on stomach and fecal samples (with small sample sizes), niche overlap has been determined as low between Blainville's beaked whales and sperm whales in the study area (Hickmott, 2005). This hypothesis can not be confirmed without ongoing investigation of the study species and of their prey.

CONCLUSION

There are two most likely possible causes for the declining trends of dwarf sperm whales and Blainville's beaked whales in the study area. Firstly, prey availability, along with factors relating to reproduction and predation, is a key determination of habitat use for deep divers (Claridge, 2006). Productivity within the Great Bahama Canyon undoubtedly has an influence of the occurrence of these deep diving species in the same way that oceanographic features are known to at other sites where deep divers are studied close to coasts. Deep diving cetaceans are dependence on particular habitats, oceanographic features and associated environmental variables. Changes in the Atlantic circulation have been demonstrated off Great Abaco Island, where waters at depth (above 1,000 m) are warming in the thermo-cline near the Bahamas (Bryden *et al.,* 2005). These deep waters can be expected to have an important influence on the foraging habitats and resulting distribution and abundance of these cetacean species in the study area. Further effort would be usefully conducted on identification of the prey species found at depth as well as on the localised current systems that influence them.

Secondly, the data used in this analysis were collected following mid-frequency sonar use during the transit of several naval vessels through the Northwest Providence Channel. Strandings associated with naval activities have previously been reported around the world. Cuvier's beaked whales appear particularly susceptible to mid-frequency naval sonar (for example, Fernández, 2006; Fernández *et al.,* 2005; Frantzis, 2004; Freitas, 2004; Balcomb and Claridge, 2001; Frantzis, 1998), yet the study species have also been involved in unusual mortality events. For example, Blainville's beaked whales stranded in the study area during the 2000 mortality event (Balcomb and Claridge, 2001) and in the Canary Islands (Martin *et al.*, 2004), dwarf sperm whales have stranded in North Carolina, US (Hohn *et al.,* 2006) and pygmy sperm whales in the Canary Islands (Martin *et al.*, 2004) coincident to naval activities. It is therefore possible that the reduction in abundance estimates in dwarf sperm whales and Blainville's beaked whales after 2000 was due to the mass mortality event that took place as a result of sonar usage in the area. However, it should be noted that effort-based observations began after the stranding event and yet estimates were highest in 2000.

It has been hypothesised that a flight response may be initiated in response to mid-frequency active sonar. Active sonar SQS-53C and SQS-56 were in use from various naval vessels for 16 hours during transit through the Northwest Providence Channel (Anon., 2001). It is therefore possible that a re-distribution of whales could have resulted from disturbance initiated by the intense noise generated by sonar use in the Channel. Sub-lethal effects can not be ruled out.

Animals have suffered embolism in other noise-related stranding events in southern Spain, around the Canary Islands and the UK (Fernández, 2006; Fernández *et al.,* 2005; Jepson *et al.,* 2003). Should the animals in the Bahamas have suffered the same, the severity of the fat emboli–induced clinical disease may have progressed over time (Fernández *et al.,* 2005 and references therein). Observed pathologies may result from a behavioural response that has adverse physiological consequences (Tyack *et al.,* 2006). Decompression-type symptoms, whilst not always lethal, can result in a more protracted syndrome leading to later death (Fernández *et al.,* 2005). Hemorrhaging was observed in the brain, ears and acoustic fats of some of the Bahamas beaked whales (Fernández *et al.,* 2005). It can be postulated that animals that did not strand immediately following the event were chronically affected but survived for some time afterwards but this is impossible to know.

The possibility that sonar usage might have resulted in the declining trend has implications for other beaked whale habitats where naval sonar usage occurs worldwide. Further analysis of the incidental observations that were collected off Great Abaco Island before the mass mortality event may provide some further useful insights.

Since the mass stranding in 2000, the US Navy has agreed not to use SQS-53C sonar in Northwest Providence Channel during peace-time (Claridge, pers. comm.). This is an appropriate precautionary step for the protection of local populations of deep diving species. This is particularly true given our current lack of understanding of the mechanisms that led to the deaths of these animals and those in other noise-induced mass strandings around the world. As a matter of urgency, and at least until we can begin to understand influences of human-induced impacts on these cetacean populations and individuals, similar measures to restrict intense noise use, and particularly mid-frequency sonar SQS-53C, should be standardised globally to protection populations of beaked whales and other vulnerable species in important habitats where these are known.

For now, the reasons for reductions in dwarf sperm whale and Blainville's beaked whale abundance estimates in the study area can not be known. However, the results of this study indicate that ongoing survey effort is important to determine the long-term abundance trends of deep divers in the study area and we now have quantitative tools to facilitate such studies.

FUTURE WORK

Covariates

Factors previously known to affect sightings rates include method of searching, species differences, group size, sea state and the cue that leads to the sighting (Barlow *et al.,* 2001), as well as sun glare (Forney, 1995; Clarke, 1986). This study included only those first-order covariates (julian day, seas state, number of scientific observers and survey start time) that were expected to influence observation rates and therefore annual abundance estimates. Other covariates that could usefully be considered for inclusion in future analysis include group size, where group synchronicity in surfacing may make the group more accessible for observation at the surface for longer (Barlow and Sexton, 1996), as well as sea surface temperature (SST) and tidal state.

In addition, deep diving cetaceans spend considerable time at depth (Baird *et al.,* 2006; Claridge, 2006; MacLeod and D'Amico, 2006; Tyack *et al.,* 2006; Barlow, 1999; Willis and Baird, 1998; Breese and Tershy, 1993), searching for cephalopods and other pelagic prey. An animal's dive time is a further limitation to detection, for example, inter-dive interval of Blainville's beaked whale averages 2 minutes (Aguilar Soto, 2006) followed by an extended foraging dive. Sperm whales exhibit long dive times (mode, 40-45 min with surface time of 8-10 min) and are often comprised of asynchronously diving 'clusters' that can be spread out over several square kilometres (Barlow and Taylor, 2005). Study of deep divers has been greatly aided with the development of sophisticated technological advances (Baird *et al.*, 2006; Aguilar Soto, 2006; Johnson and Tyack, 2003), where dive times and feeding strategies of a few individuals of Northern bottlenose whales (*Hyperoodon ampullatus*), Cuvier's and Blainville's beaked whales have become accessible with suction-cup tag development. There remains almost no information on *Kogiidae* dive times or those of the other *Ziphiidae,* yet these are known to influence detection rates (Barlow and Sexton, 1996). Improved understanding of dive patterns will increase our understanding of foraging habits and depths (Aguilar Soto, 2006) and, hence, appropriate modelling techniques.

Modelling

Interaction effects, the dependence of covariates on each other, could be usefully investigated in future analysis. Linear interactions between two covariates can be investigated by generating a new variable that is the product of two covariates (McCarthy, 2007) and can provide ecologically meaningful terms in the model. Important interaction terms are likely to include species and other sighting conditions (Barlow *et al.,* 2001). Because of the relatively sparse data currently available, interactions were not included, in order to keep the models relatively simple and functioning.

In addition, some covariates may demonstrate a non-linear relationship with abundance estimates and significant relationships may be further elucidated with generalised additive models (GAMS) in the future. Whilst GAMs are more flexible, they require more data than has been currently been collected in the study area and hence the decision was made to investigate only linear relationships in the current study.

An overdispersion parameter might be included to account for variability in the abundance estimate that is not explained by covariates. Overdispersion is variation beyond that of the assumed sampling distribution (Gelman *et al.,* 2003) and might be expected due to habitat heterogeneity and aggregation (Silechi, 2006), where cluster effects occur due to group behaviour (for example, Lonergan *et al.,* 2007; Durban, 2002). Over-dispersion would be suitably represented with a quasi-Poisson error distribution, via introduction of the overdispersion parameter, where the variance is a multiple of the mean.

Increases in model complexity (e.g. interactions, GAMS, overdispersion) come at a cost to model fitting. This cost can only be supported by relatively large datasets. In Bayesian MCMC, this cost is reflected not only in convergence problems for small datasets, but also in very flat (i.e. non-informative) posterior distributions. Here, a relatively simple model formulation (a Poisson distribution with linear effects) was chosen in order to make useful inference. However, it is important to discuss the limitations of the model, for example, only being able to detect significant linear effects of covariates. Whilst this may be unrealistic, it allows detection of strong effects where they are present. This work has detected effects that are intuitive, and consistent with existing data and knowledge of this system. Furthermore, rather than just using simple annual encounter rates as a measure of abundance, these key covariate effects have been incorporated into a formal analyses of abundance trends.

Field monitoring studies

The long term study of deep diving cetaceans can provide important information about area specific abundance estimates or trends. We don't currently know how these abundances relate to discrete populations. Over time, behavioural observations can provide information on a wide variety of behavioural and life-history traits that can influence accuracy of population and abundance estimates. Foraging strategies, predator defences, group living, mating systems, social structures and communication (Hooker *et al.,* 2002b) are all important components of small study site work. It seems likely that small scale boat work will most advance our understanding of oceanic island associated population structure, ranging and life history traits of dwarf sperm whales and Blainville's beaked whales. Such studies are critical for accurate assessment of abundance trends, and indeed population status, at the appropriate scale. Individual identification techniques can refine understanding of sociality, group structure and residency. Further photo-identification studies would compliment this data set in determining fine scale details of individual's habitat use and social structure. Indeed, photo-identification using Bayesian analysis is a novel but successful approach (Durban *et al.,* 2005).

However, deep diving species like beaked whales and sperm whales are not always associated with specific canyons (Waring *et al.,* 2001) or with slope and shelf waters (Ferguson *et al.,* 2006) and identifying offshore habitats away from oceanic islands is challenging, but necessary. Further, home ranges may be broad (McSweeney *et al.,* 2007) and interactions between island-associated populations and open ocean populations are as yet unknown. For example, sperm whales and Blainville's beaked whales are regularly found in the waters of neighbouring Bahamian islands (Moretti *et al.,* 2006). Yet, interactions between those and the study animals remain unknown. The size of the study area has clear implications on the scale and type of data collected. Species habitat associations change across spatial scales and these should be incorporated in habitat analysis to test our understanding over broader scales (Thogmartin and Knutson, 2007; Ferguson *et al.,* 2006). The scale on which we choose to monitor abundance of species has ramifications for protection mechanisms. Scale of study site is an important consideration for decision making to ensure population protection and conservation.

Therefore in parallel with localised surveys, large scale abundance surveys are important to indicate home ranges, potential hotspots of important habitats and determination of abundance estimates on appropriate scales for management. Identification and application of techniques to currently unknown offshore habitats are likely to be important for dwarf sperm whales, Blainville's beaked whales and sperm whales, particularly in areas of high or repeated anthropogenic use. Whilst data have been modelled for temporal trends and spatial variation in relative abundance, little effort has put towards a consistent framework for assessing questions of spatial variation (Royle and Wikle, 2005) and this is an important conservation consideration, particularly for little known offshore species. This may be possible through the application of hierarchical models applied at multiple sites, as have been investigated for other marine mammals (Ver Hoef and Frost, 2003), and at multiple scales for birds (Thogmartin and Knutson, 2007). However, initially more effort will be required in collecting a series of baseline survey data.

This study has contributed unique information on abundance trends of deep diving cetaceans off Great Abaco Island in the Bahamas, incorporating a series of influential explanatory covariates, to explain as much of the variability in the estimates as possible. Bayesian analysis has enabled uncertainty to be dealt with explicitly by including confidence intervals surrounding the estimates. Such analyses can now be developed over time with an increasing data set and focused survey objectives to effectively monitor deep diving cetaceans in this area.

Logging sperm whale © Diane Claridge, BMMRO

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APPENDIX A

Example of WinBUGS program, developed using BUGS language, used to investigate covariates and annuals trends in dwarf sperm whales off Great Abaco Island, Bahamas between 2000 and 2006.

```
# comments on the model precede this symbol

Data
list(years = 7,
surveys = c(12,22,19,11,4,7,5))

Initial values for 3 MCMC chains (3 chains to check for convergence)
list(mu.b.year = 4, sd.b.year=5, b.start=0, b.bss=-1, b.day=0, b.scobs=1, b.totobs=0, sd.b=1)
list(mu.b.year = 4, sd.b.year=5, b.start=0, b.bss=-1, b.day=0, b.scobs=1, b.totobs=0, sd.b=1)
list(mu.b.year = 4, sd.b.year=5, b.start=0, b.bss=-1, b.day=0, b.scobs=1, b.totobs=0, sd.b=1)

Model                          # tells WinBUGS that text within the curly brackets defines the model
{
for (k in 1:years){
for (i in 1: surveys[k]){

Kscount[i,k] ~ dpois(mu[i,k])

log(mu[i,k]) <- b.year[k] + b.day*(day[i,k]-day.cc) + b.bss*(bss[i,k]-bss.cc) + b.scobs*(scobs[i,k]-scobs.cc) +
b.totobs*(totobs[i,k]-totobs.cc)  + b.start*(start[i,k]-start.cc) # + b[i,k]
}

# covariate means

start.c[k] <- mean(start[1:surveys[k],k])
bss.c[k]<-mean(bss[1:surveys[k],k])
day.c[k] <- mean(day[1:surveys[k],k])
scobs.c[k] <- mean(scobs[1:surveys[k],k])
totobs.c[k] <- mean(totobs[1:surveys[k],k])
}

start.cc <- mean(start.c[])
bss.cc<- mean(bss.c[])
day.cc <- mean(day.c[])
scobs.cc <- mean(scobs.c[])
totobs.cc <- mean(totobs.c[])

# random effects prior for annual effects (i.e. drawn from the same distribution)

for (k in 1:years){
for(i in 1:surveys[k]){
b[i,k] ~ dnorm(0, tau.b)
}

b.year[k] ~ dnorm(mu.b.year, tau.b.year)
annual.index[k] <- exp(b.year[k])
}

mu.b.year ~ dnorm(0, 0.01)
tau.b.year <- 1/(sd.b.year*sd.b.year)
sd.b.year ~dunif(0,10)

tau.b <- 1/(sd.b*sd.b)
```

```
sd.b ~ dunif(0,10)

# single, ‘fixed effect’ priors with a normal distribution with a mean of 0 and precision (= 1/variance)

b.0 ~ dnorm(0, 0.01)

b.day ~ dnorm(0, 0.01)
prob.day <- step(b.day)

b.bss ~ dnorm(0, 0.01)
prob.bss <- step(b.bss)

b.scobs ~ dnorm(0, 0.01)
prob.scobs <- step(b.scobs)

b.totobs ~ dnorm(0, 0.01)
prob.totobs <- step(b.totobs)

b.start ~ dnorm(0, 0.01)
prob.start <-step(b.start)
}
```